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The Use of Allelochemicals of Aquatic Macrophytes to Suppress the Development of Cyanobacterial “Blooms”

Evgeny Kurashov, Julia Krylova and Elena Protopopova

Abstract

Harmful algal “blooms”, or HABs, is a hazardous natural phenomenon that often occurs under the influence of anthropogenic factors, for example, during the anthropogenic eutrophication of water bodies. An increase in the frequency and duration of cyanobacterial “blooms” carries a number of serious threats, including local and global degradation of water resources and the impact of cyanotoxins. There are various methods of fighting cyanobacterial “blooms” - physical, chemical, the use of bacterial preparations, etc. However, these methods are not effective enough and, most importantly, do not allow effectively solving the problem of suppressing HABs in water bodies without damage to other components of the aquatic ecosystem. Allelopathy is a natural phenomenon for both stimulatory and inhibitory effects of one plant upon another including microorganisms that resolves this problem. Allelochemicals of macrophytes can be considered as natural algacides and become the basis of a nature-like convergent technology to suppress the development of plankton cyanobacteria and prevent HABs in water bodies. In our work, we used some allelochemicals of aquatic macrophytes to create a combined algicide of the new generation for suppressing the development of cyanobacteria. The effectiveness of suppressing cyanobacterial “blooms” is demonstrated by the example of field experiments with mesocosms and natural phytoplankton.

Keywords: harmful algal “blooms”, phytoplankton, cyanobacteria, allelopathy, allelochemicals, field experiments, mesocosms

1. Introduction

Harmful algal “blooms”, or HABs, is a hazardous natural phenomenon that often occurs under the influence of anthropogenic factors, for example, during the anthropogenic eutrophication of water bodies. An increase in the frequency and duration of cyanobacterial “blooms” carries many serious threats, including local and global degradation of water resources and the impact of cyanotoxins [1–3]. This problem is especially relevant and acute for millions of small reservoirs widely used for various types of water consumption: fisheries and aquaculture, water supply for various industries, including agricultural, drinking, and domestic water supply, recreational purposes, including sporting events. HABs occur when algae or

cyanobacteria (most often they are) develop beyond measure and produce harmful effects on other hydrobionts, fish, aquatic and terrestrial animals, and birds as well as people [4, 5]. HABs disrupt the esthetics of water bodies and render the water unsuitable for various kinds of water uses. Economic damage due to HABs can be millions of dollars [6, 7].

Widespread HABs is a phenomenon to which special attention should be drawn since such “blooms” pose a number of serious threats, including local and global degradation of water resources and exposure to cyanotoxins [8–14].

Cyanobacterial “blooms” of water bodies are officially recognized as a global problem of modern ecology. Seasonal intense cyanobacterial “blooms” of reservoirs bring additional undesirable properties to natural and drinking water, such as a specific smell, taste, and the presence of toxins (microcystins). In some regions, the importance of this problem has been increasing recently [15]. The Working Group on the Evaluation of Carcinogenic Risks to Humans listed cyanotoxins as a carcinogenic substance harmful to humans [16].

The introduction of biotechnological methods into the practice of water body management that have maximum efficiency is one of the tasks of modern science. These include, first of all, the so-called convergent nature-like technologies, i.e. technologies that are based on any natural mechanisms causing this or that effect. These are precisely technologies that may be intended to ensure the sustainable development of modern countries [17–19].

Such technologies, aimed at managing the development of plankton communities in general and phytoplankton communities, in particular, may be based on such a phenomenon as allelopathy. This natural phenomenon can be very useful for effectively preventing and stopping the development of cyanobacterial “blooms” in water bodies [20–22]. Many existing methods of combating cyanobacteria [23] do not effectively solve the problem of “blooms” of water bodies without damage to other components of the ecosystem [3]. Usually, they are associated with serious adventitious effects on aquatic organisms and ecological systems [24].

At the same time, the application of the method of metabolic allelopathic control of HABs in water bodies during eutrophication is an effective and innovative solution to this problem. This approach preserves and restores water quality in water bodies, makes them suitable for multifunctional use, and natural allelochemicals (metabolites of macrophytes and their synthetic analogs) can be an effective alternative to existing algicides [20, 22, 25].

In reservoirs where macrophytes are developed (as a rule, at least 30% of the projective cover of the water area), water “bloom” is almost never observed. These circumstances are the causal basis for the development of nature-like technologies for the prevention and suppression of HABs with the help of new generation algicides based on allelochemical substances characteristic of aquatic macrophytes.

It has become apparent that metabolites-allelochemicals may be functioning in the processes of chemical suppressing of planktonic cyanobacteria in the aquatic ecosystems. However, data from field experiments are few concerning the effect of aquatic macrophyte allelochemicals on cyanobacteria, which is necessary for the development of nature-like technologies for preventing and suppressing cyanobacterial “blooms”, and therefore they are the objects of “hottest” areas of research. Utilization of allelochemicals from aquatic macrophytes or using their synthetic analogs to inhibit cyanobacterial overgrowth is an environment-friendly technology for suppressing HABs.

Some reviews are focusing on the practice of the application of allelochemicals in agriculture [26, 27], but the field of using nature-like allelopathic technology to manage aquatic ecosystems is still poorly developed.

In the present study, we aimed to provide the information on the suppressing of cyanobacteria by macrophytes allelochemicals and the possibility to develop an algaecide of the new generation as a convergent nature-like technology for preventing and stopping the development of HABs in water bodies based on such a phenomenon as allelopathy.

2. Suppression of the development of cyanobacteria by aquatic macrophytes

Allelopathy as a natural phenomenon had been repeatedly recorded for a very long time in the 3rd century BC in ancient Chinese literature [28]. The term “allelopathy” was coined comparatively recently, in 1937 by Austrian plant physiologist Hans Molisch [29], who can be named as the father of allelopathy [30]. In general, we can consider allelopathy as an area of science, which investigates inhibitory or stimulatory biochemical interactions between the two plant/plant or plant/microorganism species.

The recent history of the study of low molecular weight organic compounds, which are small molecules (less than 900 amu) and constitute the low molecular weight metabolic profiles of organisms, should apparently begin with the discovery of the inhibitory effect of volatile plant excreta on microorganisms by Tokin Boris Petrovitch during the experimental work of 1928–1930 [31]. The research resulted in a number of publications, in one of which (“Bactericides of plant origin (phytoncides)”) [32], the term “phytoncides” appeared. In the future, the doctrine of phytoncides was developed, which was reflected in the publication of several monographs. The history of research on phytoncides of aquatic and coastal plants began in the 40s of the XX century with the works of Gurevich Faiva Abramovich (1918–1992) [33], a student of B.P. Tokin. These studies ended in 1973 with the defense of a doctoral dissertation “Phytoncides of aquatic and coastal plants, their role in biocenoses” [34]. In particular, it was F.A. Gurevich who showed that the phytoncidal activity of aquatic plants is closely related to the macrophyte species and peculiarities of its development. He also showed that phytoncides are a very significant factor in the distribution of hydrobionts in a water body, including invertebrates.

At present, we can say that the macrophyte and algal allelopathy is paid much less attention than allelopathy in terrestrial ecosystems. Macrophytes and cyanobacteria are known to have an antagonistic relationship in different natural and experimental aquatic ecosystems [25, 35, 36].

It is a recognized fact that phytoplankton is poorly developed in macrophytic lakes. Even if we take into account the opinion that this is due to such factors as winning competition for nutrients and shading, then in the overwhelming number of cases, the main factor providing suppression of phytoplankton development is undoubtedly allelopathic suppression [37]. Apparently, the competition for nutrients cannot be recognized as a decisive factor in the outcome of the struggle between macrophytes and cyanobacteria, including considering that most aquatic macrophytes are rooted, and they usually obtain the main part of the necessary nutrients from the bottom sediments, which is characterized by high nutrient concentrations [38].

It is well known the phenomenon when shallow-water lakes can change their trophic status and the type of lake ecosystem, being either a pure water body with well-developed aquatic vegetation or a water body with low transparency, high turbidity, and intensive phytoplankton (mainly cyanobacteria) development. In other words, they can shift from one state to another [36, 39–43]. As this takes place,

the mutual inhibitory allelopathic activities of macrophytes and phytoplankton may lead to the dominance of either macrophytes or phytoplankton [44].

We observed a similar effect in a floodplain lake with a changing trophic state in the Volga-Akhtuba interfluvium, when cyanobacteria and macrophytes dominated in the same water body in different years [36]. Some evidence exists [45–48] that allelopathy is a factor affecting the development of phytoplankton (including cyanobacteria) in shallow lakes at the projective cover of macrophytes from 20 to 100%.

The importance of allelopathy as a powerful regulatory mechanism initiates a lot of studies devoted to the study of the inhibitory (sometimes stimulating) allelopathic effect of macrophytes on cyanobacteria and algae in aquatic ecosystems [49–58]. More than 60 species (67) of macrophytes are known to exhibit allelopathic activity against cyanobacteria. They are presented in **Table 1**.

According to the principle of allelopathic action, it is possible to prevent or mitigate the massive development of Cyanobacteria (blue-green algae), which leads to the HABs in water bodies. The implementation of this research direction promises huge benefits since it will solve the problem of the “blooms” of water bodies without negative consequences for other components of the ecosystem [20, 22, 25].

As follows from **Table 1**, data from laboratory studies, in general, prevail in the observation and proof of the effect of macrophyte allelopathy on cyanobacteria. These studies are based on laboratory-scale experiments using the co-cultures systems, adding plant extracts, or leachate collection. This state of affairs is associated with a more complex organization and interpretation of field studies. In this regard, data from field experiments and observations, for example with mesocosms, are of particular value. Numerous studies (including those included in **Table 1**) strongly suggest that allelopathy might thus be relevant in natural waters and suppress cyanobacteria and algae.

There are observations on the differentiation of the inhibitory effect of macrophytes on various species of cyanobacteria and algae. For example, it was concluded that the extracts, exudates, and live material of macroalgae *Chara australis* (Charophyta) exhibited strong inhibitory effects on the cyanobacterium *Trichormus variabilis* (formerly *Anabaena variabilis*), but no effect was observed on the growth of the green alga *Scenedesmus quadricauda* [82].

The available data allow us to speak about the selective inhibition of various species of cyanobacteria by allelochemicals of various species of macrophytes. As a result, the allelopathic effect of macrophyte association on cyanobacteria (and all phytoplankton) seems to be stronger than the effect of one macrophyte species. This is evidenced by the fact that, as has been shown, the allelopathic effect of excretions of the association of macroalgae (*Chara hispida*, *C. baltica*, *C. vulgaris*, *Nitella hyaline*) and *Myriophyllum spicatum* is characterized by a significantly stronger effect than the effect of monoculture of macrophytes [83]. Such a combination of selective inhibition of macrophyte allelochemicals and a more strong impact of macrophyte assemblages toward the undesired cyanobacteria may be useful for biocontrol of HABs in water bodies as well as in aquaculture to remove harmful cyanobacteria and leave other algae to be used as food for hydrobionts and fish. The author [83] suggested that different allelochemicals produced by different macrophytes may exhibit a synergistic effect concerning cyanobacteria. It was also noted in [128] that different plants produce different types of allelochemicals and in different quantities. These summarized findings are therefore provided with more probability the basis for an effective strategy for reducing cyanobacterial biomass by introducing into water bodies with mixtures of submerged or floating native macrophytes for both restorations of aquatic ecosystems and mitigation of the HABs.

Species of macrophytes	Ecological form	Study scale	Cyanobacteria inhibited	Source
<i>Acorus tatarinowii</i> , <i>Acorus calamus</i> , <i>Acorus gramineus</i>	EM	L	Cyanobacteria as a whole	[59, 60]
<i>Arundo donax</i>	EM	L	<i>Microcystis aeruginosa</i>	[51, 57, 61–63]
<i>Brasenia schreberi</i>	FM	L	<i>Anabaena flos-aquae</i>	[64]
<i>Cabomba caroliniana</i>	SM	L	<i>Microcystis aeruginosa</i> , <i>Dolichospermum flosaquae</i> (formerly <i>Anabaena flos-aquae</i>), <i>Leptolyngbya tenuis</i> (formerly <i>Phormidium tenue</i>), Cyanobacteria as a whole	[65, 66]
<i>Canna generalis</i>	EM	L	<i>Microcystis aeruginosa</i>	[67]
<i>Ceratophyllum demersum</i>	SM	L, F	<i>Microcystis aeruginosa</i> , <i>Pseudanabaena limnetica</i> (formerly <i>Oscillatoria limnetica</i>), <i>Oscillatoriales</i> , <i>Anabaena</i> sp., <i>Trichormus variabilis</i> (formerly <i>Anabaena variabilis</i>), <i>Aphanizomenon flos-aquae</i> , <i>Synechococcus elongatus</i> , Cyanobacteria as a whole	[58, 68–78]; Our data
<i>Chara aspera</i>	SM	L	<i>Anabaena cylindrica</i> , <i>Anabaena torulosa</i> , <i>Anabaenopsis elenkinii</i> , <i>Microcystis aeruginosa</i> , <i>Microcystis flos-aqua</i> , <i>Synechococcus</i> sp., Cyanobacteria as a whole	[37, 79–81]
<i>Chara australis</i>	SM	L	<i>Trichormus variabilis</i> (formerly <i>Anabaena variabilis</i>)	[82]
<i>Chara baltica</i> , <i>C. canescens</i>	SM	L	<i>Synechococcus</i> sp.	[81, 83]
<i>Chara contraria</i>	SM	L	<i>Anabaena cylindrica</i> , <i>Microcystis aeruginosa</i> , <i>Cylindrospermum</i> sp., Cyanobacteria as a whole	[79]
<i>Chara fragilis</i>	SM	L*	<i>Oscillatoria limnetica</i> , Cyanobacteria as a whole	[71]
<i>Chara globularis</i>	SM	L	<i>Anabaena cylindrica</i> , <i>Anabaena torulosa</i> , <i>Anabaenopsis elenkinii</i> , <i>Planktothrix rubescens</i> , <i>Microcystis aeruginosa</i> , <i>Microcystis flos-aqua</i> , <i>Cylindrospermum</i> sp., <i>Aphanizomenon flexuosum</i> , Cyanobacteria as a whole	[68, 72, 79, 84]
<i>Chara hispida</i>	SM	L, F	Cyanobacteria as a whole	[83, 85]
<i>Chara rudis</i> , <i>Chara tomentosa</i> , <i>Chara delicatula</i>	SM	L	<i>Anabaena cylindrica</i> , <i>Anabaena torulosa</i> , <i>Anabaenopsis elenkinii</i> , <i>Planktothrix agardhii</i> , <i>Planktothrix rubescens</i> , <i>Microcystis aeruginosa</i> , <i>Microcystis flos-aqua</i> , <i>Cylindrospermum</i> sp., <i>Aphanizomenon flexuosum</i> , Cyanobacteria as a whole	[79]
<i>Chara vulgaris</i>	SM	L, F	<i>Anabaena torulosa</i> , <i>Anabaenopsis elenkinii</i> , <i>Microcystis aeruginosa</i> , Cyanobacteria as a whole	[79, 83, 86, 87]
<i>Cyperus alternifolius</i>	EM	L	<i>Microcystis aeruginosa</i>	[67]

Species of macrophytes	Ecological form	Study scale	Cyanobacteria inhibited	Source
<i>Eichhornia crassipes</i>	FM	L	<i>Microcystis aeruginosa</i> , <i>Microcystis</i> sp., <i>Raphidiopsis raciborskii</i> (formerly <i>Cylindrospermopsis raciborskii</i>), <i>Arthrospira platensis</i> (formerly <i>Spirulina platensis</i>), <i>Nostoc linckia</i> (formerly <i>Nostoc piscinale</i>), Cyanobacteria as a whole	[88–91]
<i>Eleocharis acicularis</i>	SM	L	Cyanobacteria as a whole	[66]
<i>Eleocharis microcarpa</i>	SM	L	<i>Anabaena flos-aquae</i> , <i>Oscillatoria tenuis</i>	[92, 93]
<i>Elodea canadensis</i> , <i>Elodea nuttallii</i> , <i>Elodea</i> sp.	SM	L, F	<i>Microcystis aeruginosa</i> , <i>Anabaena</i> spp., Cyanobacteria as a whole	[35, 68, 78, 94, 95]
<i>Hydrilla verticillata</i>	SM	L	<i>Dactylococcopsis</i> sp., <i>Microcystis aeruginosa</i>	[56, 58, 96]
<i>Egeria densa</i>	SM	L	<i>Microcystis aeruginosa</i> , <i>Dolichospermum flosaquae</i> (formerly <i>Anabaena flos-aquae</i>),	[66]
<i>Limnophila sessiliflora</i>	SM		<i>Microcystis aeruginosa</i>	[66]
<i>Myriophyllum aquaticum</i>	SM	L	<i>Microcystis aeruginosa</i>	[97]
<i>Myriophyllum brasiliense</i> , <i>Myriophyllum alterniflorum</i> , <i>Myriophyllum heterophyllum</i>	SM	L	<i>Microcystis aeruginosa</i> , <i>Dolichospermum flosaquae</i> (formerly <i>Anabaena flos-aquae</i>)	[98]
<i>Myriophyllum elatinoides</i>	SM	L	<i>Microcystis aeruginosa</i>	[99]
<i>Myriophyllum spicatum</i>	SM	L, F	<i>Microcystis aeruginosa</i> , <i>Dolichospermum flosaquae</i> (formerly <i>Anabaena flos-aquae</i>), <i>Leptolyngbya tenuis</i> (formerly <i>Phormidium tenue</i>); Cyanobacteria as a whole	[54, 65, 71, 78, 83, 100–104]
<i>Myriophyllum verticillatum</i>	SM	L	Cyanobacteria as a whole	[105, 106]
<i>Najas marina</i>	SM	L	<i>Anabaena</i> sp., <i>Trichormus variabilis</i> (formerly <i>Anabaena variabilis</i>), <i>Synechococcus elongates</i> , Cyanobacteria as a whole	[74, 94]
<i>Nasturtium officinale</i>	EM	L	<i>Microcystis aeruginosa</i>	[107]
<i>Nelumbo nucifera</i>	FM	L, F	<i>Microcystis aeruginosa</i> , Cyanobacteria as a whole	[108, 109]
<i>Nitella gracilis</i> , <i>Nitella opaca</i> , <i>Nitellopsis obtusa</i> , <i>Nitella hyaline</i> , <i>Nitella</i> sp.,	SM	L, F	<i>Nitzschia palea</i> , <i>Anabaena cylindrica</i> , <i>Anabaena torulosa</i> , <i>Anabaenopsis elenkinii</i> , <i>Microcystis flos-aquae</i> , <i>Cylindrospermum</i> sp., <i>Aphanizomenon flexuosum</i> , Cyanobacteria as a whole	[68, 79, 83]
<i>Nuphar lutea</i>	FM	L, F	Cyanobacteria as a whole	[110]; Our data

Species of macrophytes	Ecological form	Study scale	Cyanobacteria inhibited	Source
<i>Nymphaea candida</i>	FM	F	Cyanobacteria as a whole	Our data
<i>Oryza sativa</i>	EM		Cyanobacteria as a whole	[111]
<i>Phragmites communis</i>	EM	L	<i>Microcystis aeruginosa</i> , <i>Phormidium</i> sp.	[108, 112]
<i>Pistia stratiotes</i>	FM	L	<i>Synechococcus leopoliensis</i> , <i>Microcystis aeruginosa</i> ,	[113–115]
<i>Potamogeton crispus</i>	SM	L, F	<i>Trichormus variabilis</i> (formerly <i>Anabaena variabilis</i>), Cyanobacteria as a whole	[82, 116, 117]
<i>Potamogeton cristatus</i>	SM	L	<i>Microcystis aeruginosa</i>	[58]
<i>Potamogeton oxyphyllus</i>	SM	L		[66]
<i>Potamogeton lucens</i>	SM	L, F	<i>Microcystis aeruginosa</i> , Cyanobacteria as a whole	[58, 71], Our data
<i>Potamogeton maackianus</i>	SM	L	<i>Microcystis aeruginosa</i>	[58, 118, 119]
<i>Potamogeton malaianus</i>	SM	L, F	<i>Microcystis aeruginosa</i> , <i>Oscillatoria</i> sp.	[118–120]
<i>Potamogeton natans</i>	SM	L, F	<i>Microcystis aeruginosa</i> , Cyanobacteria as a whole	[78], Our data
<i>Potamogeton pectinatus</i>	SM	L	<i>Microcystis aeruginosa</i> , <i>Oscillatoria tenuis</i>	[76, 118, 121]
<i>Ranunculus aquatilis</i>	SM/FM	L	<i>Microcystis aeruginosa</i>	[107]
<i>Ruppia maritima</i>	SM	L	<i>Microcystis aeruginosa</i>	[122, 123]
<i>Stratiotes aloides</i>	FM	L, F	<i>Synechococcus elongatus</i> , <i>Microcystis aeruginosa</i> , Cyanobacteria as a whole	[49, 68, 71]
<i>Typha latifolia</i> , <i>Typha minima</i> , <i>Typha angustata</i>	EM	L	<i>Dolichospermum flosaquae</i> (formerly <i>Anabaena flos-aquae</i>), <i>Romeria leopoliensis</i> (formerly <i>Synechococcus leopoliensis</i>), <i>Microcystis aeruginosa</i>	[57, 124–126]
<i>Vallisneria denseserrulata</i> , <i>Vallisneria spiralis</i> , <i>Vallisneria spinulosa</i>	SM	L	<i>Microcystis aeruginosa</i>	[58, 66, 75, 127]

Table 1.
The number and relative content (% of total essential oil) of the fatty acids in some species of freshwater macrophytes and macroalgae from different water bodies.

Lombardo et al. [129] suggested that lake trophic state and extent of submerged vegetation coverage maybe the most important factors during formation in situ macrophyte–phytoplankton patterns at a large scale of natural water bodies. In this case, with a larger projective cover, a greater allelopathic effect will be achieved [45–48].

Not all macrophytes have the same allelopathic effect on cyanobacteria. Macrophytes that have the greatest suppressive effect on cyanobacteria (taking into account, among other things, information from **Table 1**) are such species

and groups as *Cabomba caroliniana*, *Myriophyllum spicatum*, *Ceratophyllum demersum*, *Elodea canadensis*, *Nuphar lutea*, *Stratiotes aloides*, and family Characeae ([22, 36, 49, 65, 71, 103, 130], etc).

In the study [131], it was concluded that of all the 15 tested aquatic macrophytes, *Nymphaea odorata* and *Brasenia schreberi* have the highest allelopathic potential. However, this conclusion was obtained in experiments with lettuce sprouts, and not with cyanobacteria. These macrophytes inhibited 78% and 82% of lettuce seedling radicle growth and 98% and 68% of *L. minor* frond production respectively. Elakovich S. D. and Wooten J. W. [132] also reported that *Nuphar lutea* has high allelopathic activity.

Similar results were obtained with the macrophytes *Potamogeton maackianus*, *Potamogeton wrightii*, and *Potamogeton crispus*, which exhibited different inhibitory effects on the two species of algae [128]. There is a view that most allelochemicals are released during the early developmental stage of plants. It is assumed that during this period, plants are most dependent on stress conditions and competition with other surrounding plants for resources such as light, nutrients, and water [133]. However, in our studies, we found that the active synthesis of allelochemicals in aquatic macrophytes can continue even at later stages of plant development [22].

For the sake of completeness, it should be noted that some terrestrial plant materials (for example, barley straw) exhibit a strong allelopathic effect on cyanobacteria under certain conditions [134–136], which is no coincidence, since terrestrial plants also contain numerous allelochemicals [28]. It was shown in [137] that salcolin (two enantiomers that differ in their anti-cyanobacterial abilities) is the key allelochemical in barley straw's which exhibits an inhibitory effect on cyanobacteria and could be used as an agent in the control of cyanobacterial HABs. A review of typical terrestrial allelopathic plants with algistatic or algicidal effects is presented in [24].

3. Anti-cyanobacterial allelochemicals produced by aquatic macrophytes

Low-molecular-weight anti-cyanobacterial allelochemicals produced by aquatic macrophytes are very diverse. They belong to different classes of chemical compounds and are functionally diverse. Allelochemicals from the following groups of chemical compounds are the most important [22, 30, 55]: aldehydes, ketones, ethers, terpenes and terpenoids, phytoecdysteroids, fatty acids, sulfur-containing compounds, nitrogen-containing compounds, alcohols, lactones, polyacetylenes, quinines, phenolics, cinnamic acid and its derivatives, coumarins, flavonoids, tannins. These groups include hundreds of allelochemicals inhibiting cyanobacteria and algae [24], which should be discussed in detail in a special review.

These allelochemicals can be extracted from the plant biomass, but also their synthetic counterparts can be produced and used. This will reduce the consumption of natural plant resources. The effectiveness of synthetic allelochemicals can be similar to their natural counterparts. Thus, synthetic allelochemicals are a hopeful alternative to the use of natural metabolites-allelochemicals against HAB-forming cyanobacteria [20, 21].

Realizing that it is impossible to consider all groups of allelochemicals, here we will focus on considering only fatty acids and phenolic compounds as the most promising (in our opinion) for biotechnological use in the fight against HABs.

Studies of potential biological activities of major low molecular weight organic compounds of aquatic macrophytes using the QSAR method [138, 139] have shown that fatty acids and gallic acid are characterized by various types of bioactivity with

the highest probability of manifestation ($P_a > 0.9$) that can induce cyanobacteria growth suppression. Further studies based on the results obtained suggest clarifying experimental studies of the reaction of various species of cyanobacteria to the effects of selected allelochemicals.

As it was received in laboratory experiments conducted with fatty acids for their effect on the cyanobacteria *Synechocystis aquatilis* and *Aphanizomenon flos-aquae*, and which are described in detail in [140], selected allelochemicals (linoleic, heptanoic, octanoic, tetradecanoic, hexadecanoic, and gallic acids) possess inhibitory allelopathic activity against cyanobacteria. However, their inhibitory effect was different. The highest values of the Suppression index (SI, defined as the cyanobacterial density in control divided by the cyanobacterial density in an experiment with allelochemicals) ($SI > 10$) were recorded (in ascending order) for hexadecanoic, linoleic, tetradecanoic, gallic acids, and a mixture of four allelochemicals (heptanoic, octanoic, tetradecanoic and gallic acids).

The highest SI values for *Synechocystis aquatilis* were obtained when the culture of cyanobacteria was exposed to gallic acid ($SI = 30$) and a mixture of heptanoic, octanoic, tetradecanoic, and gallic acids ($SI = 35.3$). *Aphanizomenon flos-aquae* was found to be more sensitive to the effect of the given mixture of allelochemicals. SI for it on the 23rd day of the experiment was 17495 [140].

In works [141, 142] problems have been raised concerning effective algal inhibitors and control HABs. To address these issues, the authors suggested using unsaturated fatty acid (linoleic acid) in conjunction with alginate – chitosan microcapsule technology. They demonstrated that the linoleic acid microsphere had good encapsulation efficiency and release property. Besides, linoleic acid sustained-released microspheres could inhibit *Microcystis aeruginosa* (Cyanobacteria) growth to the non-growth state, and thus linoleic acid microsphere may be used as a potential candidate for HABs control.

Studies on the use of microgranules saturated with an allelochemical or a combination of allelochemicals (for example, a combination of fatty acids and phenolic compounds) to suppress cyanobacteria look very promising. The inhibitory agent, gradually releasing from the microgranules, prolongs its allelopathic effect on cyanobacteria. A sustained-release time of allelochemicals can range from 40 to 120 days [142–144]. A review of the studies carried out in this direction is presented in [128]. Results obtained in different investigations open up new promising areas for scientific research and practical use of allelochemicals of aquatic macrophytes.

According to results received in [112], nonanoic acid can inhibit the growth of cyanobacteria *Leptolyngbya tenuis* (formerly *Phormidium tenue*) and *M. aeruginosa*, whereas, no inhibitory effects of stearic, and palmitic acids was found.

In earlier works [113, 125], it was also found, that three fatty acids (α – linolenic, linoleic, and an unidentified C8:2) inhibited cyanobacteria (particularly T 625 *Romeria leopoliensis* (formerly *Synechococcus leopoliensis*) and T 1444 *Dolichospermum flosaquae* (formerly *Anabaena flosaquae*)).

The essential oil of some allelopathic plants (*Potamogeton cristatus*, *Potamogeton maackianus*, *Potamogeton lucens*, *Vallisneria spirulosa*, *Ceratophyllum demersum*, and *Hydrilla verticillata*) was demonstrated to inhibited *Microcystis aeruginosa*, during which fatty acids constituted an important part of the essential oils isolated.

Recently, Wang et al. [95] reported the inhibitory effects of some fatty acids on *Microcystis aeruginosa*. The authors stated that pentadecanoic acid, linoleic acid, alpha-linolenic acid, and stearic acid were the most potent allelochemicals from *Elodea nuttallii* along with dihydroactinidiolide and beta-ionone.

We showed [140] that such plants as *Potamogeton natans*, *Nuphar lutea*, *Nymphaea alba*, *Myriophyllum spicatum*, *Persicaria amphibia* are the most active producers of allelochemical fatty acids, and therefore they can have a significant

allelopathic effect on cyanobacteria and phytoplankton in total. In these plants, the proportion of fatty acids in the content of volatile organic compounds can exceed 60–70%.

Our studies of the metabolome of *Potamogeton perfoliatus* from different habitats in Lake Ladoga show that the abundance of cyanobacteria in the associations of this macrophyte depends on the content of carboxylic acids in a given plant (**Figure 1**).

The study by Gao et al. [145] demonstrates that nonanoic acid may be involved in synergistic interactions with other allelochemicals, demonstrating a stronger allelopathic effect against *Microcystis aeruginosa*.

Similar results were obtained for octadecanoic acid [146], which may participate in synergistic, antagonistic, and additive allelopathic interactions. These findings led to the conclusion that joint effects of different allelochemicals depend on various factors such as the chemicals used, their respective proportions, the total concentration of the mixture, and the receptor species [146].

In addition to fatty acids, among allelochemicals, special attention should be paid to phenolic compounds.

As early as in 1981 [100], the results were published, which demonstrated that phenolic compounds extracted from *Myriophyllum spicatum* exhibit algicidal activity against cultured algae and natural phytoplankton assemblages. Later, it was found that such aquatic macrophytes as representatives of the genus *Myriophyllum* are able to excrete polyphenol-like allelochemicals to inhibit the growth of green algae and cyanobacteria [98]. A number of identified polyphenols (ellagic, gallic, pyrogallic, and catechin) and fatty acids (hexadecanoic acid, stearic acid, α -linolenic acid) were shown to significantly suppress the development of HAB-forming cyanobacteria species [147, 148].

Additionally, a study [78] has revealed that the major allelochemicals identified in tested macrophyte ethyl acetate extract of *Nasturtium officinale* included quercetin, tannic acid, and gallic acid. Also, findings are the combinations of different types of polyphenols, such as pyrogallic acid, gallic acid, and ellagic acid may have

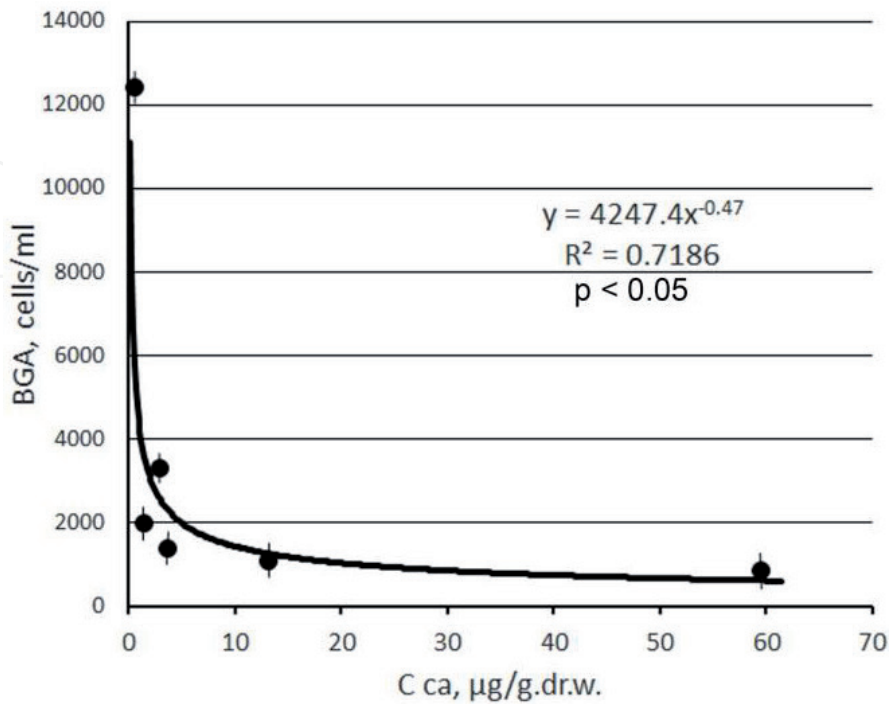


Figure 1. Dependence of the concentration of cyanobacteria (BGA, cells/ml) on the concentration of fatty acids (Cca, µg/g.dr.w.) in *Potamogeton perfoliatus* in Lake Ladoga.

an additive or synergistic effect on cyanobacterium *Microcystis aeruginosa* and the joint action of phenolic allelochemicals may be an important allelopathic pattern of submerged macrophytes to inhibit the growth of HAB-forming cyanobacteria in natural aquatic ecosystems [53, 146, 148–150].

In a study [54] during the investigation of contributions of five allelochemicals, (+) catechin, eugenin, and ellagic, gallic, and pyrogalllic acid, in the allelopathic effects of *Myriophyllum spicatum* on the cyanobacterium *M. aeruginosa* it was observed that these compounds, on average, may provide up to 50% of the allelopathic effects of *M. spicatum*. According to results received in [112], four phenols (sinapic, syringic, caffeic, and gallic acids) inhibited the growth of cyanobacteria *Leptolyngbya tenuis* (formerly *Phormidium tenue*) and *M. aeruginosa*. The inhibitory effect of pyrogalllic acid and gallic acid produced by *M. spicatum* in relation with cyanobacteria was also demonstrated in [53, 114].

It is beyond question that there is a huge amount of scientific material regarding the allelopathic properties of fatty acids and gallic acid ([52, 54, 56, 67, 88, 103, 112, 113, 118, 119, 124–126, 146, 148, 151–166], etc.). This circumstance gives every reason to use them to create a new generation of algicides based on allelochemical substances of aquatic macrophytes. The use of this information, as well as the results of our researches [36, 138, 140], formed a prerequisite for the development of a new generation algicide based on allelochemicals of aquatic macrophytes against cyanobacteria. It is precisely fatty acids (heptanoic, octanoic, tetradecanoic acids) and gallic acid that were included in its composition [167].

4. Mesocosm study of the effects of allelochemicals on cyanobacteria

Evidence of suppression of the development of phytoplankton, including planktonic cyanobacteria, in real natural conditions by traditional observations, even in the most obvious cases [36], is nevertheless indirect and often contradictory [48, 168]. Taking this into account, the way of assessing the effect of allelochemicals on cyanobacteria in experiments with mesocosms in natural conditions is more promising and makes it possible to obtain results corresponding to natural aquatic ecosystems.

A good example is a field study by Hilt et al. [169] in which the authors found an allelopathic effect of the macrophyte *Myriophyllum verticillatum* on natural phytoplankton (including cyanobacteria) in Lake Krumme Lake (Berlin, Germany). In a mesocosm study [170] in Laguna Blanca lake in Manantiales (Maldo-nado, Uruguay) it was observed that macrophytes species (*Egeria densa* and *Potamogeton illinoensis*) seem to exert strong biological effects on phytoplankton biomass, and they are able to keep phytoplankton biomass low through allelopathic influence, even in the absence of zooplankton grazing.

In another mesocosm study [171], similar results were obtained, demonstrating that another species of the genus *Myriophyllum* (*Myriophyllum spicatum*) under conditions of 85 l mesocosms during 13 days of exposure had an only short-term inhibitory effect on total phytoplankton and green algae, whereas consistent negative effects (allelopathic) were detected concerning *M. aeruginosa*.

After the development of an algicide containing fatty acids (heptanoic, octanoic, tetradecanoic acids) and gallic acid, the rationale for the use of which is presented in detail in [140], we conducted the first experiments with this algicide with natural phytoplankton communities under conditions mesocosms.

In the field experiments, mesocosms with a volume of 700 liters were used. The experiments were carried out on two ponds on the territory of St. Petersburg (Russia): at Pulkovo Pond (pond 1; coordinates 59.835899, 30.328642) and Aviator's

Pond (Pond 2; coordinates 59.868343, 30.300443). The depth of the ponds at the location of the experiments was about 3 m. The mesocosms were filled with water from the pond, then algicide was added to them in an amount so that its concentration in the water of the mesocosms was 1 mg/l.

In Pulkovo Pond, the experiment was carried out from June 25 to July 5, 2019. In the Aviatorov Pond, the experiment was carried out from July 2 to July 16, 2019. The temperature and light conditions in the mesocosms corresponded to those in the water of the pond outside the mesocosms. The change in water temperature in the surface layer of the studied ponds is shown in **Figure 2**.

The results of the algicide impact on the phytoplankton of pond 1 are shown in **Figures 3–6**.

As can be seen from **Figure 3**, in the water of pond 1, both the abundance and the biomass of all phytoplankton increased during the experiment. At the same time, this was not observed in the mesocosm. In the first three days, a decrease in phytoplankton biomass without a change in its abundance occurred. Subsequently, the abundance and biomass of phytoplankton in the mesocosm remained approximately at the same level as they grew in the pond. By the end of the experiment (on the 11th day), the phytoplankton biomass in the pond exceeded that in the mesocosm by about 5 times, and the abundance - by almost 12 times. The greatest differences were observed on the 8th day of the experiment; the difference in biomass and abundance was 7 and 20 times, respectively. Thus, the action of an algicide based on fatty acids and gallic acid inhibited the growth of phytoplankton.

The data of phytoplankton analysis are confirmed by the data on the measurement of optical density in the pond and the mesocosm (**Figure 4**). By the end of the experiment, an increase in optical density in the pond and a significant decrease in optical density in the mesocosm were observed (**Figure 4**). By the end of the experiment, the difference was about 2.3 times. This was also noticeable visually: the water in the mesocosm was more transparent than the water in the pond surrounding the mesocosm (**Figure 5**).

It is interesting to trace how the quantitative indicators of cyanobacteria in the pond and the mesocosm changed. *Dolichospermum solitarium* (formerly *Anabaena solitaria*) was the dominant cyanobacterial species in the pond (and at the beginning of the experiment in the mesocosm). This species belongs to cyanobacteria

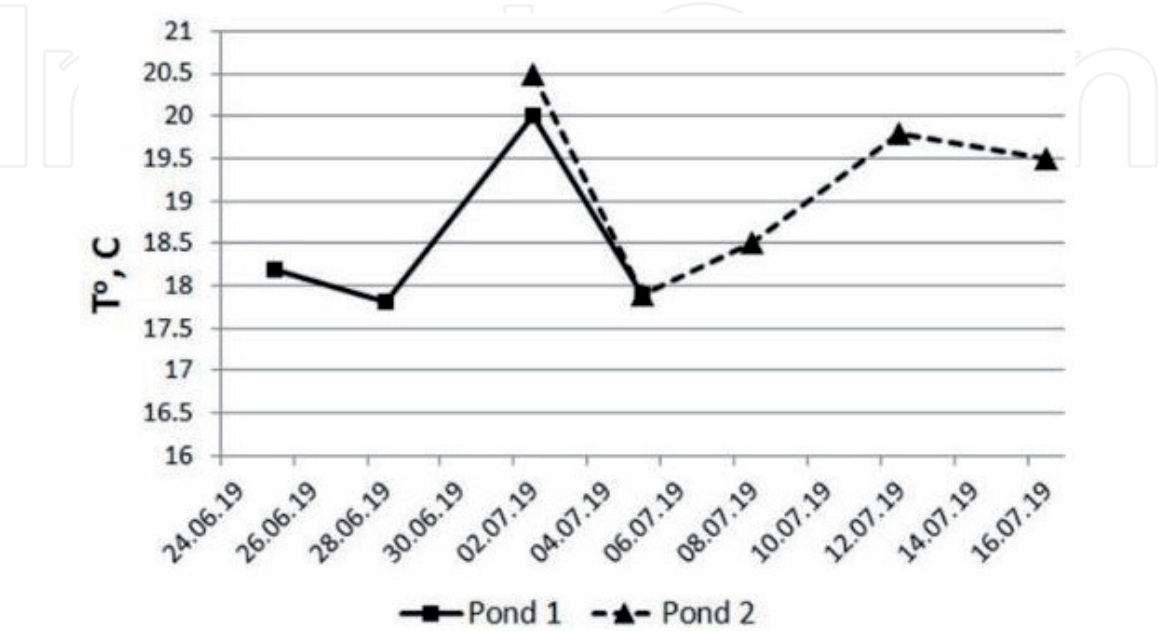


Figure 2.
Change in water temperature (° C) in the surface layer of the investigated ponds.

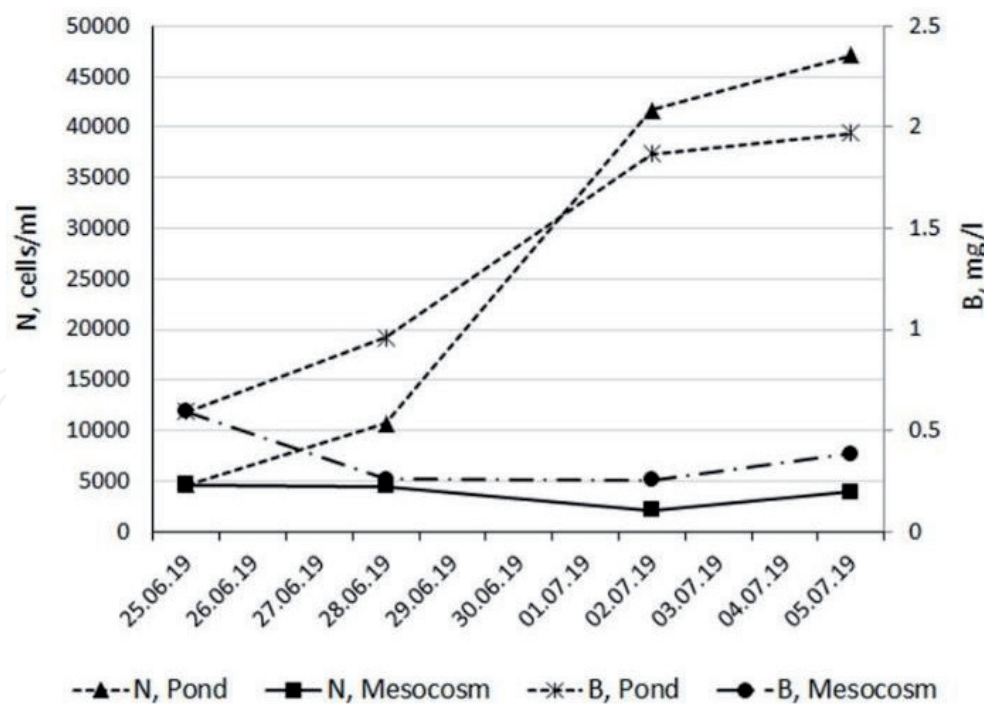


Figure 3.
Changes in the abundance and biomass of total phytoplankton in pond 1 and the mesocosm under the influence of algicide with a concentration of 1 mg/l.

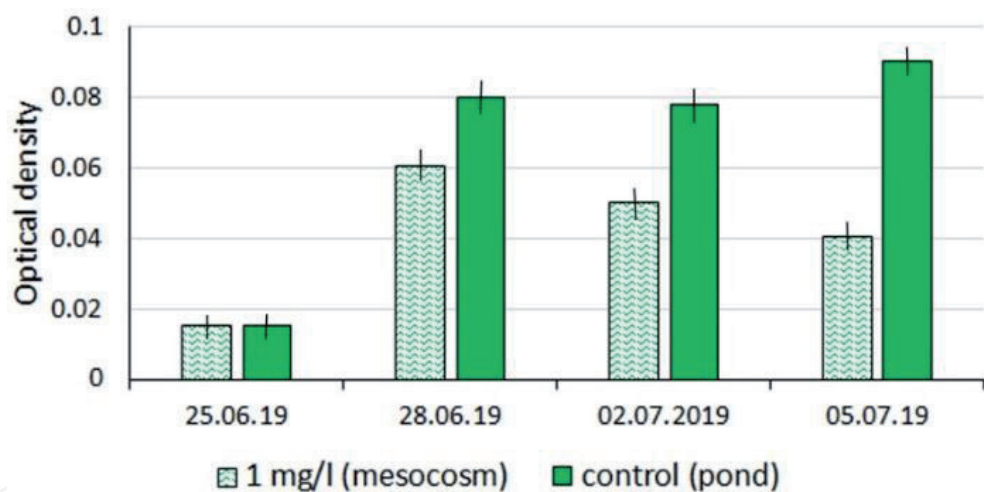


Figure 4.
Change in the optical density of the water mass in pond 1 and the mesocosm when exposed to algicide with a concentration of 1 mg/l.

capable of causing the phenomenon of HABs [172]. A decrease in both the number and biomass of cyanobacteria both in the pond and in the mesocosm was observed on the third day of the experiment. Moreover, in the mesocosm, this decrease was more pronounced. Subsequently, an increase in the number and biomass of cyanobacteria both in the pond and in the mesocosm was observed. However, it was more intense in the pond. By the end of the experiment (on the 11th day), the biomass of cyanobacteria in the pond exceeded that in the mesocosm by about 2.5 times, and the number - by 1.5 times. The greatest differences were observed on the 8th day of the experiment, the difference in biomass and abundance was 4.4 and 39 times, respectively. At the end of the experiment, the same species *Dolichospermum solitarium* remained the dominant species in the composition of cyanobacteria. At the same time, *Cuspidothrix ussaczewii* (formerly *Aphanizomenon elenkinii*) began to dominate in the mesocosm among cyanobacteria. This species is also included in



Figure 5.
The contrast in the state of water mass in pond 1 and mesocosm 4 (a) and 11 (B) days after exposure to algicide.

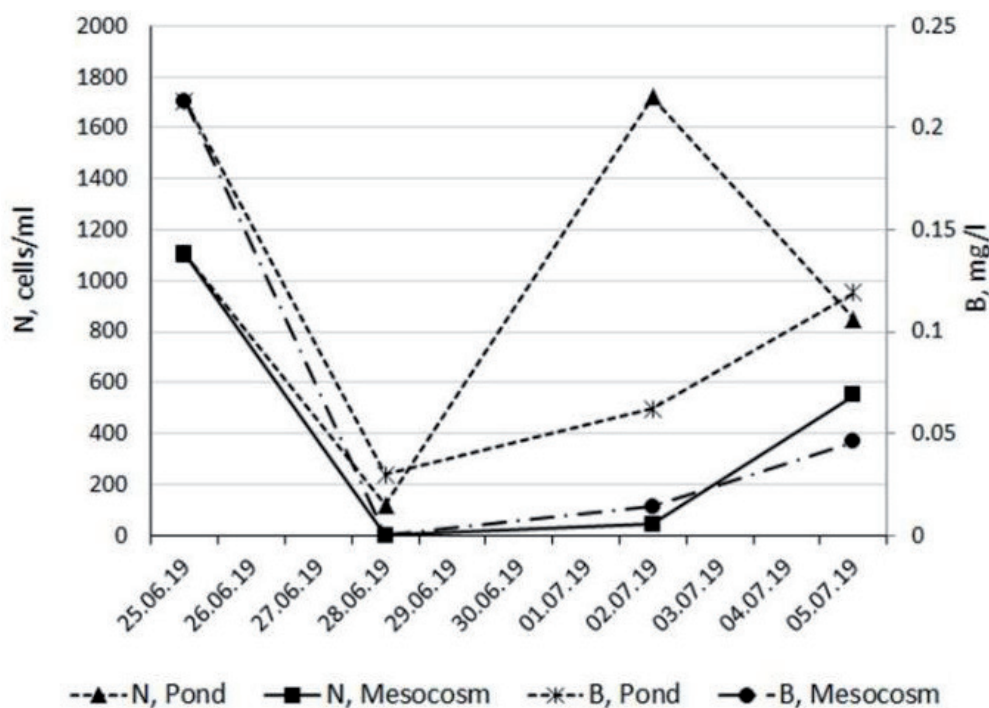


Figure 6.
Changes in the abundance and biomass of cyanobacteria in pond 1 and the mesocosm upon exposure to algicide at a concentration of 1 mg/l.

the bloom-forming Cyanobacteria from water bodies of the North-Western Russia list [173]. However, *C. ussaczevii* is less toxic than *D. solitarium*, for which toxigenic strains producing delayed-action toxins have been isolated [174].

Thus, the action of an algicide based on fatty acids and gallic acid prevented the growth of the number of cyanobacteria and changed their species structure.

In pond 2, the beginning of the experiment coincided with an intense cyanobacterial “bloom” (Figure 7), while their biomass was more than 55 mg/l. At the same time, in the surface layer of the pond, the maximum water temperature (20.5°C) for the entire duration of the experiment was noted (Figure 2). The cyanobacteria *Aphanizomenon flos-aquae*, *C. ussaczevii*, and *Dolichospermum affine* (formerly *Anabaena affinis*) dominated in phytoplankton. *Aphanizomenon flos-aquae* is one of the most widespread species that form HABs in ponds and lakes in Northwest Russia [173]. The species is capable of synthesizing dangerous (including for humans) toxins [173]. *Cuspidothrix ussaczevii* also often causes water



Figure 7.
Cyanobacterial HAB in pond 2 and water-filled mesocosm on July 2, 2019.

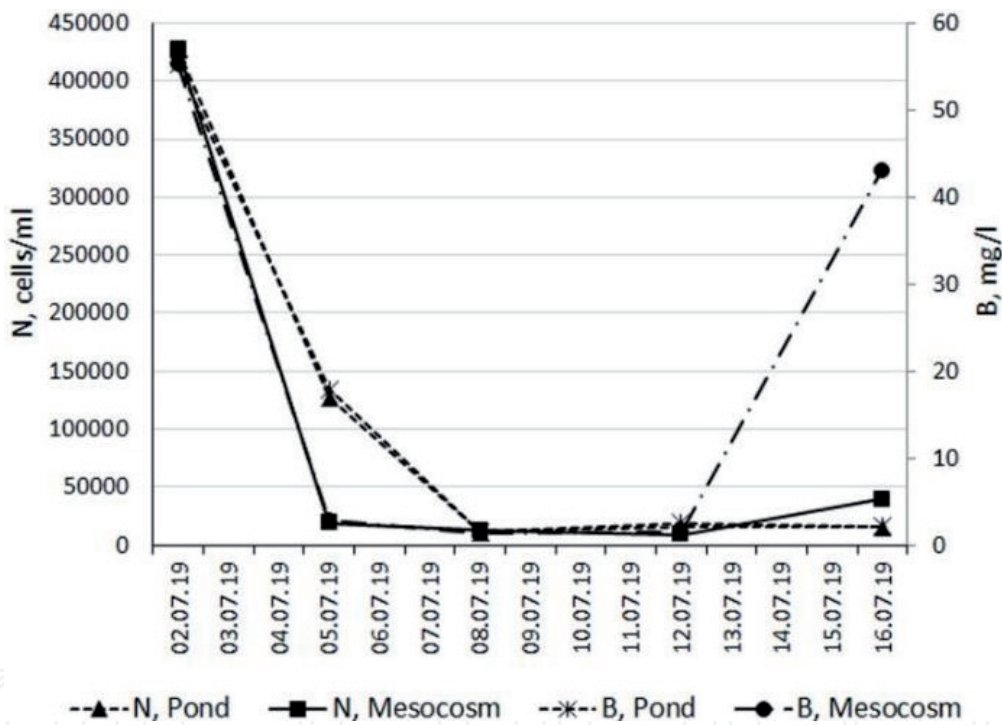


Figure 8.
Changes in the abundance and biomass of total phytoplankton in pond 2 and the mesocosm under the influence of algicide with a concentration of 1 mg/l.

“bloom” in water bodies of St. Petersburg and the Leningrad Region, being the dominant or subdominant in bloom-forming cyanobacteria [173].

By the fourth day of the experiment, the water temperature in the pond dropped to about 18°C. This led to a decrease in the number and biomass of cyanobacteria, apparently, mainly due to their sinking into the lower layers of the reservoir. However, an even greater decrease in the development of cyanobacteria was observed in the mesocosm, in which cyanobacteria could not sink so deeply (**Figure 8**). This is also confirmed by data on the optical density of water in the pond and in the mesocosm, where a more significant decrease was noted (**Figure 9**). Subsequently, the optical density slightly decreased to approximately the same level in the pond and mesocosm and almost did not change in the pond and mesocosm.

At the same time, the control of the development of cyanobacteria from pond 2 in the laboratory, where there was no decrease in temperature, showed their significant growth in the control. With that, under the influence of allelochemicals, significant suppression of plankton growth was observed, recorded by optical density (Figure 10).

By the 8th day of the experiment, a further decrease in the optical density of plankton under the influence of algicide was noted in the laboratory. At the same time, a decrease in optical density and the control was observed, obviously, due to the inability of natural plankton to laboratory conditions (the experiment was carried out in 0.5-liter jars).

By July 8, the species of cyanobacteria *Aphanizomenon flos-aquae* and *Cuspidothrix ussaczevii* in the mesocosm dropped out of the dominant composition, although they continued to dominate in the pond water. As our laboratory experiments with this algicide have shown [140], this species of cyanobacteria was especially sensitive to the used mixture of allelochemicals. So, a complete suppression of the development of the culture of *Aphanizomenon flos-aquae* was observed in the experiment with the combined effect of heptanoic, octanoic, tetradecanoic, and gallic acids at various concentrations (0.1, 1, and 10 mg/l).

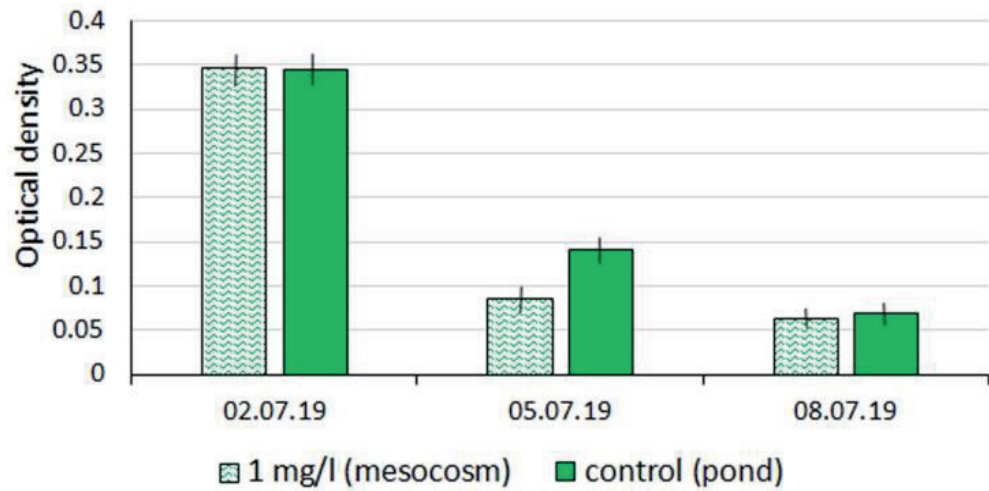


Figure 9. Change in the optical density of the water mass in pond 2 and the mesocosm when exposed to algicide with a concentration of 1 mg/l.

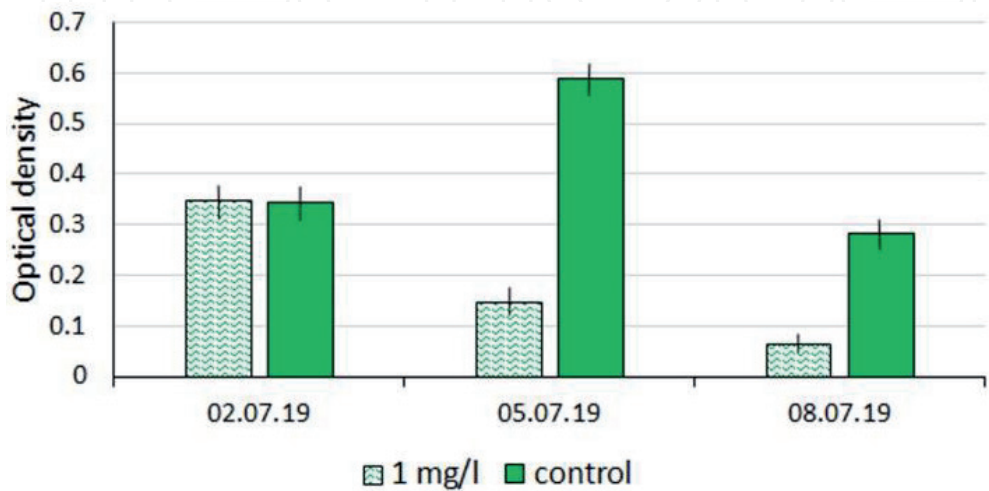


Figure 10. Change in the optical density of the water mass in pond 2 and the mesocosm when exposed to algicide with a concentration of 1 mg/l during exposure in the laboratory.

In the last phase of the experiment (from July 12), representatives of Cryptophyta - *Cryptomonas* sp., *Komma caudata* (formerly *Chroomonas acuta*) dominated the pond in the composition of phytoplankton (**Figure 11**). Among the cyanobacteria, *Aphanizomenon flos-aquae* and *Aphanocapsa conferta* dominated. In the mesocosm at this time (especially toward the end of the experiment) cryptophyte algae (98% of the total phytoplankton biomass) with the dominant *Cryptomonas* sp. reached a very high development (with biomass of more than 42 mg/l) (**Figure 11**). Cyanobacteria were represented by the species *Dolichospermum affine*, *Aphanocapsa conferta* with very little quantitative development.

It is noteworthy that by the end of the experiment in the mesocosm, the total phytoplankton biomass returned to almost the same high values as at the beginning of the

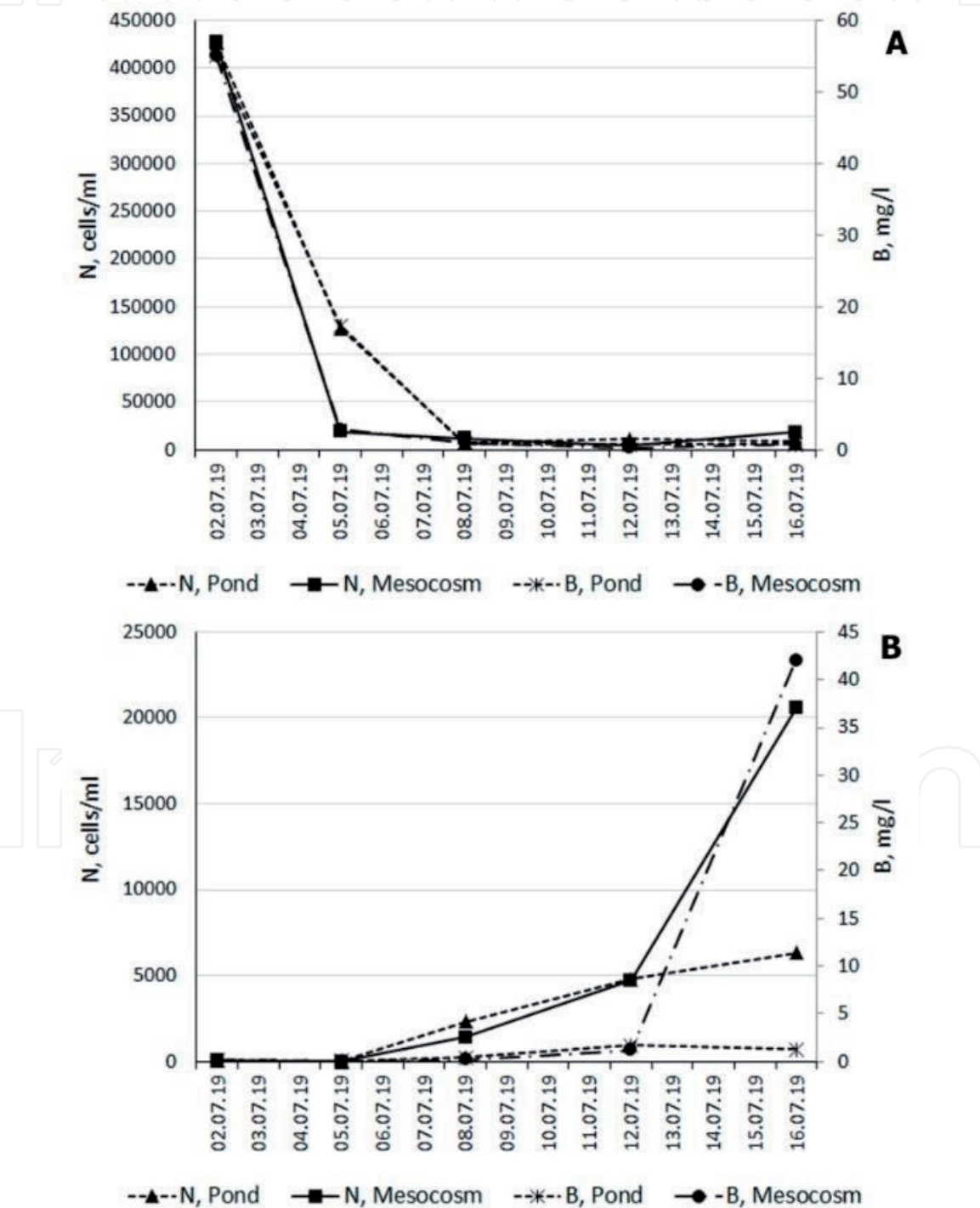


Figure 11.
Changes in the abundance and biomass of cyanobacteria (a) and Cryptophyta (B) in pond 2 and the mesocosm under the influence of algicide at a concentration of 1 mg/l.

experiment. However, if at the beginning of the experiment cyanobacteria prevailed (about 99% of the total biomass of phytoplankton), then by the end of the experiment cryptophyte algae accounted for more than 98% of the biomass of phytoplankton. *Cryptomonas sp.* dominated among cryptophyte algae. That is, the replacement of dangerous toxicogenic species of cyanobacteria with cryptophyte algae occurred, which can be consumed by aquatic organisms and which are safe for other organisms, including humans. If we project this result to entire aquatic ecosystems, then we can get a very beneficial ecosystem effect, expressed in the suppression of HABs and the development of algae, whose production can be consumed, for example by zooplankton and planktivorous fish.

Thus, the main results of the experiments carried out on the effect of an algicide of four allelochemical components (heptanoic, octanoic, tetradecanoic, and gallic acids) on the phytoplankton of natural water bodies can be considered the following results, indicating that allelochemical substances of aquatic macrophytes: 1) are able to effectively reduce phytoplankton development and suppress even intense HABs; 2) may lead to the replacement of dangerous cyanobacteria in phytoplankton with safe algae, whose production can be used in the food chains of aquatic organisms.

5. Conclusions and perspectives

In this way, available data show that the use of allelochemicals from aquatic macrophytes to inhibit cyanobacterial overgrowth is an environment-friendly and perspective technology for suppressing HABs. Allelochemicals can be considered as natural algicides and become the basis of a nature-like convergent technology to mitigate the development of plankton cyanobacteria and prevent HABs in water bodies.

One can quite agree with the conclusion of work [24] that allelopathy is a promising strategy to control HABs as the effectiveness of allelochemicals on inhibiting microalgae cells has been discovered, investigated, and confirmed in many works and for many years [175]. However, there are several problems that must be investigated in order to understand what determines the strength of the manifestation of the allelopathic effect. One of these problems is undoubtedly the action of various environmental factors.

Another problem is the resistance of allelochemicals in the aquatic environment and their chemical or biochemical (under the influence of bacteria) changes [26, 74, 168, 176]. In this regard, very promising are works in which systems are being developed that allow dosing and prolonging the release of allelochemicals into the aquatic environment [141–143].

The development and research of allelopathy and its application for suppressing the HABs are striving toward a future for sustainable, rational, and effective using the water resources worldwide. The algicides of the new generation developed based on the phenomenon of allelopathy can definitely reduce the amount of synthetic algicides and herbicides used.

While allelochemicals have shown growth inhibition of planktonic cyanobacteria, there is still insufficient knowledge of the impact on various species of cyanobacteria (especially their action in real aquatic ecosystems), the influence of various factors on the action of allelochemicals, and the molecular mechanisms of their action. These gaps may limit their use as conventional biotechnology for the mitigation and prevention of HABs in aquatic ecosystems.

All the laboratory studies can propose only the potential for allelopathy of macrophytes metabolites toward cyanobacteria, its real use as biotechnology for the management of planktonic communities and HABs will be possible only after convincing field studies using mesocosms and entire ecosystems.

In addition, if we are to understand more about the mechanisms of allelochemicals actions that cyanobacterial cells respond to, more cognizance needs to be taken of the molecular peculiarities of interactions between allelochemicals and cyanobacterial cells.

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Conflict of interest

The authors declare that there is no conflict of interest.

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