toxins

Review

Cyanobacteria and Macroinvertebrate Relationships in Freshwater Benthic Communities beyond Cytotoxicity

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Abstract: Cyanobacteria are harmful algae that are monitored worldwide to prevent the effects of the toxins that they can produce. Most research efforts have focused on direct or indirect effects on human populations, with a view to gain easy accurate detection and quantification methods, mainly in planktic communities, but with increasing interest shown in benthos. However, cyanobacteria have played a fundamental role from the very beginning in both the development of our planet's biodiversity and the construction of new habitats. These organisms have colonized almost every possible planktic or benthic environment on earth, including the most extreme ones, and display a vast number of adaptations. All this explains why they are the most important or the only phototrophs in some habitats. The negative effects of cyanotoxins on macroinvertebrates have been demonstrated, but usually under conditions that are far from natural, and on forms of exposure, toxin concentration, or composition. The cohabitation of cyanobacteria with most invertebrate groups is long-standing and has probably contributed to the development of detoxification means, which would explain the survival of some species inside cyanobacteria colonies. This review focuses on benthic cyanobacteria, their capacity to produce several types of toxins, and their relationships with benthic macroinvertebrates beyond toxicity.

Keywords: cyanobacteria; cyanotoxins; benthos; macroinvertebrates; detoxification; accumulation

Key Contribution: The biological role of cyanobacteria in benthic habitats remains to be determined. Harmful bioaccumulation of cyanotoxins in benthic macroinvertebrates depends on the type of exposure. Cyanobacteria in benthic habitats not only affect grazers but also shredders and collectors. Detoxification processes could explain the different tolerance capacity of macroinvertebrates.

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Citation: Ubero-Pascal, N.; Aboal, M. Cyanobacteria and Macroinvertebrate Relationships in Freshwater Benthic Communities beyond Cytotoxicity. *Toxins* **2024**, *16*, 190. https://doi.org/10.3390/toxins16040190

Received: 29 February 2024
Revised: 1 April 2024
Accepted: 9 April 2024
Published: 15 April 2024

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1. Introduction

Most published works on the interrelationships between cyanobacteria and other freshwater organisms tend to demonstrate and quantify the harmful effect of cyanobacteria and how other freshwater organisms attempt to survive them [1,2]. However, the stress situations that cause massive cyanobacteria growth and the associated toxicity are usually extraordinary in ecosystems: floods, droughts, eutrophication, deforestation, water temperature changes, competition for nutrients, etc. [3]. Toxic events where cyanobacteria can be found or are involved are not new, but have occurred since ancient times. For example, molecular studies have revealed the presence of cyanotoxins in sediments dating back to the ancient Mayan culture (550–1200 years ago), and are associated with algal bloom episodes [4]. References to color changes to fresh water associated with fish mortality appear in the Book of Exodus and are collected in 12th-century manuscripts in Scotland, in which monks refer to these episodes as "sick lochs" [5] More recently, animal poisoning or deaths related to cyanobacteria toxicity have been noticed worldwide, with examples in Australia [6] and Poland [7]. In a climate or global change context, the stress situations that trigger the toxic response of cyanobacteria will probably become more frequent and harmful worldwide in the future [8] and will continue to be extraordinary. Despite their controversial reputation, cyanobacteria are among the first inhabitants on our planet, and have contributed to create favorable environmental conditions for life on Earth and its diversification [9], and have established numerous symbiotic relationships with other organisms, from unicellular eukaryotes to aquatic and terrestrial metaphytes and metazoans [10]. They also play a determinant role in the maintenance of freshwater ecosystems, especially lotic ones, but this aspect is still poorly understood [11].

Cyanobacteria can be collected and might live in a wide variety of habitats, including extreme conditions, because of their adaptations in nutrient storage, N fixation, buoyancy, formation of resting cells, UVR-protective compounds or the production of wide sheaths [9]. It is important to remember that blue–green algae may capture atmospheric nitrogen (N) in either specialized cells (heterocytes) or vegetative cells in special environmental conditions. Cyanobacteria's capacity to produce cyanotoxins was acquired very early on. Molecular sediment studies evidence the presence of microcystins (MCs) and cylindrospermopsin (CYN) 4700 years ago [12] and that of saxitoxins (SXT) 2.1 billion years ago [13]. This ability to synthesize toxins was missed or retained by different taxa during the group's phylogenetic history [14].

The keenest interest shown in cyanotoxin studies has always been related to planktonic species, such as animals (including humans) that depend on reservoirs and lakes for water supply, yet this fact might lead to some bias in the knowledge and interpretation of cyanotoxicity. For instance, besides believing that cyanotoxins are linked with stress conditions in high eutrophic masses of water, the presence of these compounds has also been reported in unpolluted calcareous rivers and oligotrophic reservoirs and lakes [15–18]. Although our understanding of benthic cyanobacterial species' diversity and distribution in freshwater streams is improving worldwide, their ability to produce cyanotoxins has been poorly studied.

Among living organisms, cyanobacteria are one of those that produce a high diversity of toxins, which vary in terms of both their molecular nature and their main effects. Of cyanotoxins, MCs and nodularins (NODs) have been thoroughly studied, more than 246 isoforms of MCs have been identified [19], and both are cyclic peptides with hepatotoxic activity. However, cyanobacteria may also produce: alkaloids, such as CYN, with hepatotoxic, cytotoxic, dermatotoxic, and even possible carcinogenic properties [20]; anatoxins, mainly anatoxin-a (ATX-a), with neurotoxic capacity [21]; SXT, which are one of the most potent naturally-occurring neurotoxins, but have been associated only with marine environments and Dinophyta until quite recently [22]; and BMAA (β-N-methylamino-L-alanine), a neurotoxic nonprotein amino acid related to several neurodegenerative diseases [23].

Vertebrate exposure to toxins occurs mainly through drinking water or food consumption [20], with recreational water use as a secondary route in humans. The effects of cyanotoxins on other organisms have been reported, and are positive or negative depending on the species, taxonomic group, or environmental conditions [24,25]. Nonetheless, experimental design is sometimes not representative of what is expected to be found in nature in terms of toxin concentration or potential synergistic or antagonistic relationships if the production of several toxins happens at the same time [26]. As most data from toxicological studies refer to very high concentrations (most unlikely under natural conditions) and atypical exposure routes, future efforts should be made to observe environmentally relevant concentrations and oral and chronic exposures [26,27] to gain a clearer idea of the risks that biota and populations face.

The bioconcentration of toxins along food webs has long since been considered one of the major environmental problems. Apparently however, it does not always occur and biodilution might happen [28,29]. The intensity or frequency of both phenomena is poorly known. However, the heterogeneous bioaccumulation levels that benthic macroinvertebrates present, the different forms of exposure to cyanotoxins to which they are subjected, and the purification and detoxification processes that are beginning to be known will condition the transfer capacity of toxicity in the freshwater food chain, and even its export to the terrestrial food chain [30–32].

This review focuses on benthic cyanobacteria and their capacity to produce several types of toxins, the dependence of aquatic macroinvertebrates on benthic cyanobacteria, their biological relationships beyond toxicity, and future perspectives.

2. Results

2.1. Benthic Toxicity

The detection of MCs in benthic cyanobacteria was reported for alpine lakes in situations related to domestic animal deaths in 1997 [15]. At the beginning, most researchers thought that this was an exceptional case. However, when more people became interested in benthos, toxicity reports increased worldwide. Today, we know that benthic toxicity is widespread in all continents (geological units) and in all, or almost all, sorts of habitats [33], ranging from lagoons, rivers, springs, peat bogs and caves to a wide range of geographical and environmental conditions. This is consistent with the fact that cyanobacteria may colonize all types of substrata in all climatic and environmental conditions (except for low-pH waters), and toxicity is likely to be much more commonplace than previously thought. The concentration of toxins is always relatively low, but the presence of several variants is common in most producer genera.

Wood et al. [2] compared the number of publications on benthic and planktonic cyanotoxicity. Although references to benthic communities have considerably increased lately, there is still a huge difference between them. If we make a comparison of continents, the image is similar, with North America and Europe presenting higher number of publications on benthic cyanotoxins (Figure 1) but with numbers still very far from planktic studies.

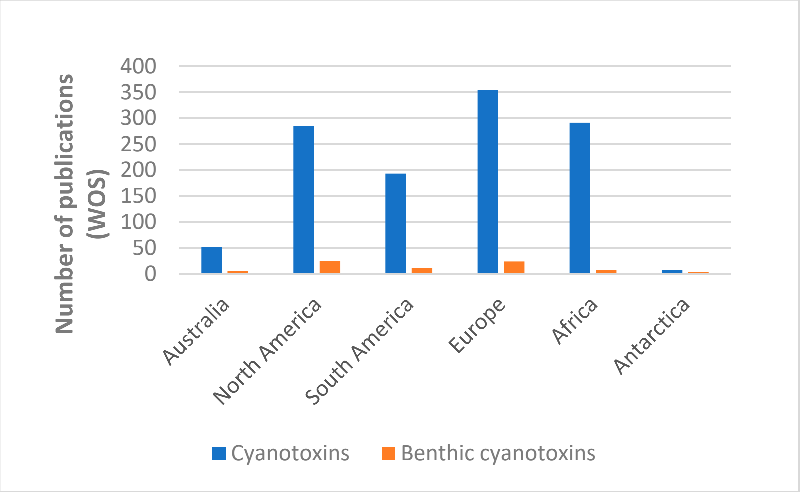

Figure 1. Distribution of papers published from 1997 on cyanotoxins and benthic cyanotoxins referring to continents or geological units.

The level and concentration of toxicity and toxins vary vastly in different countries. China and Canada host water bodies with the highest level of MCs [34], much higher than the World Health Organization's permissible level of 1 µg/L. In fact, countries like Canada and Australia have raised the admissible MC concentration for drinking water to 1.5 and 1.3 µg/L, respectively [35,36], but the US National Center for Environmental Assessment claims that the WHO drinking-water guideline value should be lower [37].

Comparison of quantitative data from the literature poses a problem, because neither raw materials (from the field or grown in the laboratory) nor the identification and quantification methodology (biochemical or genomic) is similar. In any case, current evidence for the spread of benthic cyanotoxicity is overwhelming.

Limnological or phycological studies have traditionally focused on lentic habitats, and lotic environments have usually been much less studied [2]. However, almost all possible cyanotoxins have been reported in rivers (Figure 2), and the number of studies that detect several toxic compounds in the same benthic samples is increasing [38–43]. It is not uncommon to find that several toxic congeners are present in the same localities and biofilms, and subdominant taxa sometimes produce higher concentrations of toxins [43–46]. This highlights the need to monitor not only biofilms where cyanobacteria are dominant.

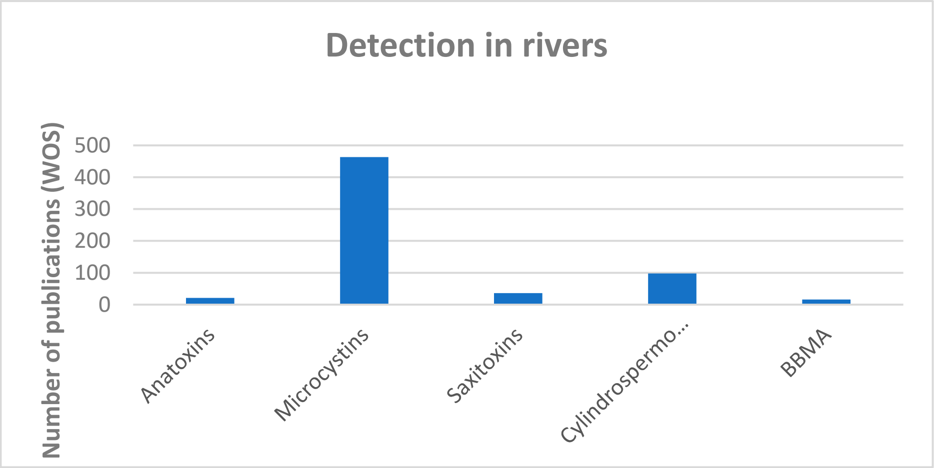

Figure 2. Papers published from 1997 related to the main groups of cyanotoxins and their detection in rivers.

Even when the parameters promoting toxin production are very likely the same, the factors involved in toxin release may differ vastly between lentic and lotic habitats, especially if the high diversity of aquatic system typologies is considered. Most lotic habitats are exposed periodically to drought and floods, and not only does their physiognomy change, but they have a marked effect on destruction and potential toxin release [9].

The detection of MCs in alpine lakes [15] was probably the first reference to MCs under oligotrophic conditions. The presence of toxins in oligotrophic calcareous rivers was reported later, and a correlation was then found between cyanobacteria biofilm toxicity and macroinvertebrate diversity by the *Photobacterium phosphoreum* test [47]. Several MC variants were identified in the same rivers, and significant negative correlations were found between the total intracellular MC content and air temperature, flow, and depth, while dissolved MCs increased with low depth and high flows but showed no significant correlation [17]. This scenario suggests a potential relationship with several environmental and climate-related variables rather than eutrophication, as confirmed later by paleolimnological data [48–50].

Heterocystous cyanobacteria (Nostocales) may fix N from the atmosphere and become independent of the N concentration of water [51], but Oscillatoriales and Chroococales can also do this under conditions with a low oxygen concentration [52,53]. However, the responses of fixing and non-fixing organisms to N/P ratios are sometimes paradoxical [54]. As the latter authors stated, the main problem is probably expecting homogeneous behavior in such a diverse group of organisms.

2.2. Multitoxic Biofilms

Most research efforts have focused on the effect of selected toxins, and not on what is probably the commonest case in nature: the presence of several toxins at the same time [38]. The potential synergy among cyanotoxins or the presence of other unknown toxic compounds cannot be ruled out, because the toxic effects of extracts are always stronger than pure toxic compounds [44,45].

Cyanobacteria blooms and biofilms are usually formed by several different strains, with potentially distinct requirements, and are both toxic and nontoxic, although the toxic ones are usually less frequent [55]. Detecting several toxic compounds in the same benthic community is also becoming increasingly common: Bouma-Gregson et al. [40,41] quantified MCs and anatoxin-a (ATX) in the Eel River (Angelo Coast Range Reserve, CA, USA). Carpenter [42] identified and quantified SXT, MCs, ATX and CYL in different taxa from the Clackamas Basin in Oregon (USA). Fadness et al. [38] quantified ATX, CYL, MC, NOD and SXT in benthic cyanobacteria in several Northern California rivers (samples from 2016–2019). The neurotoxins anatoxin-a (ATX), SXT and BMAA have also been reported from freshwater cyanobacteria [22,56–58]. No clear relationship to nutrients and cyanotoxicity has been found, as some other authors suggest [59].

Saxitoxin has been reported previously only from marine habitats, and anatoxin and BBMA are only known to be produced by freshwater (or soil) cyanobacteria [58,60]. However, we are now aware that saxitoxin and anatoxin have a widespread distribution, with reports on every continent, except Antarctica [22], but their distribution will very likely grow when more research has been conducted. BMAA seems to be present in all the morphological cyanobacteria groups from freshwater, brackish and marine environments [58]. As far as we know, there is no information about the effects of these toxins on river biota, but BMAA is related to several neurodegenerative diseases and STX has not been related to any human intoxication to date [1,58].

2.3. The Role of Mucilage

Mucilage production is important in the formation of cyanobacteria biofilms and colonies attached to rocks in river riffles. Mucilage might also play a role in the retention of nutrients and water (upon emersion), but it would seem that it can also retain toxins, as shown by Young et al. [61] and Marco et al. [62], who followed immunological methods. The retention of toxins by mucilage also seems to be common in other toxic groups, such as Dinophyta (very common in marine habitats) [63] and might represent a defense mechanism.

The relationship of mucilage and phosphorus (P) deficiency and the activity of phosphatases (mono- or diesterases) have been verified in several algal and plant groups [64,65]. It is important for the survival of all microalgae, including cyanobacteria, in calcareous habitats where P is retained in carbonate deposition.

2.4. Toxicity and Taxonomy

The generalization of applying the analysis of sequences to ensure the identity of organisms has revolutionized the taxonomy of all groups, including cyanobacteria, where the scarcity of diagnostic characteristics has always been a big problem and a challenge for taxonomists.

The implementation of a multiphasic approach with taxonomic, biochemical, ecological, and genomic information has been proposed in an attempt to gain a more complete image of taxa and their requirements [66], but this path has not been followed by all scientists. In the last few years, the genus *Nostoc* has been split into 15 genera: *Aliinostoc*, *Amazonocrinis*, *Atlanticotrix*, *Compactonostoc*, *Dendronalium*, *Desikacharya*, *Desmonostoc*, *Halotia*, *Komarekiella*, *Mojavia*, *Minunostoc*, *Parakomarekiella*, *Pseudoaliinostic*, *Purpureonostoc* and *Violetonostoc*. In addition, multiple new species have been described, with more than 100 recognized [67,68], which confirms much higher diversity than previously thought. Thus, caution is recommended when interpreting the literature to take into account nomenclatural changes. Without a clear morphological description or images, and no genomic information available, it is difficult to be sure of the names indicated in papers, and it is even more difficult to accurately make comparisons of toxicological aspects.

Can we now be sure that similar morphotypes belong to the same species and have a similar chemical composition and the ability to produce, or not, toxins?

Conspicuous *Nostoc pruniforme* colonies play an important role in the physiognomy and development of benthic communities in some lakes or rivers, and they may produce toxins. Recently, Carpenter [42] reported the presence of several different types of toxins in this species. In some Greenland lakes, *N. pruniforme* develops very big monospecific communities that produce toxins, which are released in different ways: grazing, active release, high nutrient concentration or physical disturbance [69].

There is a clear parallelism with calcareous streams, where floods that can seasonally occur destroy colonies and mats by releasing intracellular toxins [70].

2.5. Relationships to Benthic Macroinvertebrates

The biological relationship between animals and cyanobacteria in freshwater ecosystems remains intricate despite the numerous published studies that share both terms, or their derivatives, as keywords (Figure 3). Most of these papers tend to study the noxious effect (mainly lab-induced) of cyanobacteria on animals, their bioaccumulation or their possible transfer through the food chain [1,2,71]. Vertebrates, including humans, are the main group in which cyanotoxicity has been studied. If we focus on aquatic species, references accumulate from fish, while information about freshwater invertebrates is scarce (Figure 3), especially about benthic fauna [3,72]. However, very little is known about the role that benthic cyanobacteria–animal relationships play in the proper functioning of freshwater ecosystems, even though they have normally cohabited in these habitats for a long time [2]. Indeed, the role played by cyanobacteria in freshwater ecosystems must definitely be more important and complex than their simple capacity to produce toxins and to be harmful for other organisms [1].

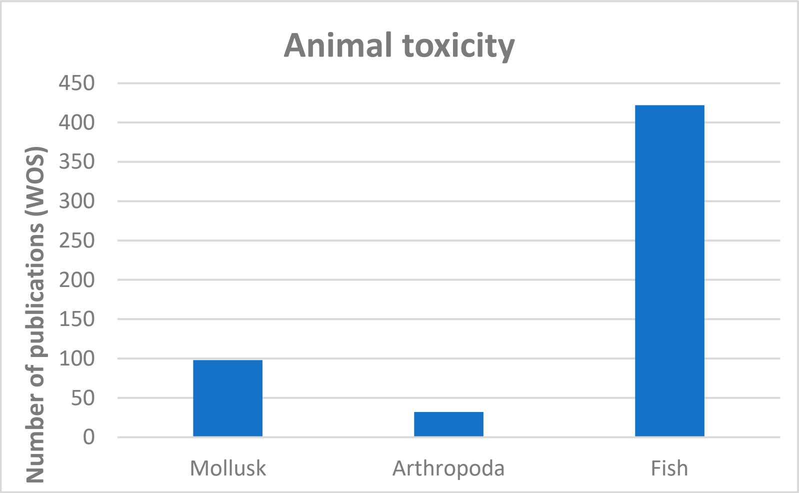

Figure 3. Papers published from 1997 related to the effect of cyanotoxins on different group of animals.

Dudley et al. [73] proposed three possible pathways of ecology interrelationships among macroalgae, including cyanobacteria colonies, and macroinvertebrates in benthic stream ecosystems: (a) food source; (b) altering the habitat's physical conditions, and even generating new ecological niches; and (c) competing for space. Food sources seem to be the principal interaction between cyanobacteria and invertebrates, and defense against grazing is one of the probable causes for which cyanobacteria may produce and secrete toxins to the environment [74,75]. Some authors consider this factor to be the least important [2]. Cyanobacteria are important primary producers from aquatic systems and can sometimes, in special environmental or seasonal circumstances, represent the main autotroph group and be the only food resource for freshwater invertebrates [76–78]. Calcareous oligotrophic rivers are colonized most of the year by a diverse cyanobacterial community, especially in Mediterranean areas [11,17]. Cyanobacteria have been traditionally considered a poor food resource, not only because they may produce toxins or present morphologies that are unappealing or difficult to ingest, such as long or thick filaments or mucilage, but also because they have been considered to be of low nutritional quality [74,79–81]. However, cyanobacteria contain nutrients and active macromolecules, such as pigments, carbohydrates, lipids (including essential fatty acids), proteins, vitamins, and minerals, which are necessary for the growth and maturation of macroinvertebrates [76,77,81–83]. A gut content analysis (microscopy, serology or DNA) has proven that certain grazer invertebrates feed on cyanobacteria [30,78,83–92], and they even prefer filamentous species [84,86,90,93], but their ingestion in other grazers may accidentally occur because some cyanobacteria species are usually found as epiphytes of macrophytes, or as part of complex biofilms, periphyton and detritus [2,3,83,94,95]. This dichotomy has led us to wonder whether the simple detection of cyanobacteria in grazers' gut contents can be nutritionally considered by proposing an enzyme analysis as the most appropriate way to confirm that invertebrates have the capacity to digest cyanobacteria and to absorb their nutrients [84]. Cases of undigested cyanobacteria being eliminated in feces are described, and the culture of such debris may inform about the digestibility of ingested cyanobacteria [96,97]. Nevertheless, as certain cyanobacteria are able to fix atmospheric N, the nutritional value of cyanobacteria in some invertebrates, and also for the whole food web, has been revealed by studies of stable carbon (C) and N isotopes [81,95,98–100]. Studies of protein and lipids, especially fatty acid biomarkers, have also confirmed that cyanobacteria are essential for macroinvertebrate survival, especially in winter when no other food is within reach [70,95]. Benthic macroinvertebrates can eat cyanobacteria from benthos and plankton [101,102].

The trophic relationship between cyanobacteria and benthic invertebrates should not be limited only to grazers, but extended to detritivores. Deposits of decomposing organic matter in freshwater ecosystems may contain cyanobacteria in the form of living colonies and organic debris or by-products, such as their toxins [80,103,104]. Although some cyanotoxins released to the environment can be degraded through physical processes, such as photodegradation, other cyanotoxins might remain active for long periods of time when they reach sediment [1,105–107]. Furthermore, this detritus is the main way for benthic invertebrates to encounter planktonic cyanobacteria or their toxins, especially in lentic habitats (lakes, dams, reservoirs, etc.) or larger rivers after bloom episodes. Stepanian et al. [108] consider the presence of cyanotoxins in sediment to be one of the factors that could explain the decline of some benthic macroinvertebrates in lakes. Woller-Skar et al. [107] noted three factors that increase the likelihood of planktonic cyanobacteria in benthos: (a) incomplete spring recruitment; (b) falling out of suspension during the growing season; and (c) remaining viable after burial. Therefore, shredder and collector macroinvertebrates can also ingest cyanobacteria because they do not usually discriminate detritus components in food, which appear in gut contents as a minority component [84,91]. Some of them, however, show preferential food selection for cyanobacteria mats [86]. The microorganisms present in detritus, such as fungi and bacteria, play a fundamental role in not only the degradation and stabilization of organic matter, which is necessary for its assimilation by some detritivores, but also in the detoxification caused by the presence of cyanotoxins, especially MCs [109,110]. Several freshwater environmental microorganisms are capable of completely degrading MCs, and even of acting on their adda ring, and different enzymatic pathways have been found. Nonetheless, the most studied pathway is that by which microcytinase (MlrA) forms a part and involves a cluster of four genes (mlrABCD) [109,111,112].

The relationship between cyanobacteria and benthic macroinvertebrates is not only trophic, but they can also interact biologically by simply living in the same habitat. As is known, invertebrates can be affected by cyanotoxins through their ingestion, either diluted in water and associated with particles (sediment or cyanobacterial cells) or by contact and diffusion through integument, eggs or gill membranes [30,86,97,101–103,107]. The harmful effect of this cohabitation has been studied more in plankton than in benthic invertebrates [72,94]. The colonial forms of cyanobacteria or assemblages with other algae in complex mats can act as effective ecological niches, which can be exploited by macroinvertebrates. Some macroinvertebrates develop territorial behavior on cyanobacteria mats [79,113], while others prefer living among cyanobacteria colonies as a form of defense [72,113,114] or settle on top of them to be more exposed to currents or the water column [73]. In the most extreme case, a few macroinvertebrate species, such as chironomid *Cricotopus* spp., must live in *Nostoc* spp. colonies to survive by establishing a mutualistic relationship: the midge obtains shelter and an unlimited source of food, and cyanobacteria gain a fixation to substrate thanks to the silk secreted by larva, an increased photosynthesis surface and higher dispersive capacity [85,93,96,114–117]. Other dipteran species, like Ephydridae, can pierce cyanobacterial mats to live in them and condition the physiostratigraphy of soil on the shores of lakes, even on a geological scale [118]. Oncoids (calcareous stromatolites produced by cyanobacteria) and vertical rocky substrates (freshwater walls extensively colonized by cyanobacteria) constitute real small-scale ecosystems where a complex biocenosis, with a high diversity of invertebrates, establishes its own trophic relationships [114,119]. Moreover, algae composition or abundance in benthic habitats may condition macroinvertebrate biodiversity [94], and vice versa [79], but this ecological aspect has been poorly studied.

Benthic cyanobacteria produce all the types of cyanotoxins described in planktonic cyanobacteria, namely, hepatotoxins (MCs, NODs and CYN), neurotoxins (SXT, ATX-a and homoanatoxin-a) and dermatotoxins (lyngbyatoxin) [2,44,69,94], which cause different kinds of damage in benthic macroinvertebrates; e.g., molecular, cellular, tissue, metabolic, functional, developmental, etc. [2,32,105,120,121]. Interestingly, hepatopancreas seems to be the main target organ in Crustacea and Mollusca independently of cyanotoxins [2,30,99,101,122–125], but only occurs in muscle when toxin exposure thresholds are reached [30]. Curiously, some studies have highlighted that most cyanobacteria extracts, and even those species or strains that do not produce toxin, are more harmful than purified cyanotoxins by showing that cyanobacteria contain other toxic compounds beyond known toxins [2,31,90,123]. Toxicity in cyanobacteria is not taxa- but clone-related, and by considering the polyphyly in some genera like *Nostoc*, it should be elucidated if toxin producers and nonproducers belong to the same species [126]. Studies have already shown that the same species can produce toxins, or not, and even the same species may produce different toxins according to the geographical location or the physic-chemical parameter of habitats [2,80]. Although less studied than zooplankton, the harmful effects of cyanotoxins on benthic habitats depend on toxin type, invertebrate species or life cycle instars. However, the negligible presence or absence of mortality of some macroinvertebrates exposed to free cyanotoxins or cyanobacteria extracts, or which feed directly on cyanobacteria toxic strains, has suggested that they present a different degree of sensitivity, tolerance or resistance, and even certain species specificity [74,81,102]. Delaney and Wilkins [127] noted that the lethality of MCs for several land insects (larvae and adults), also observed in freshwater invertebrates, occurs in the long term after exposure or ingestion compared to mammals. This finding demonstrates the existence of differences in sensitivity or tolerance of animals to the toxicity of cyanotoxins. Crustacea, for instance, have survival rates of 100%, even for exposures to concentrations of cyanotoxins like those in bloom episodes [30,128]. Long-term macroinvertebrates exposure to cyanotoxins via feeding may involve bioaccumulation levels higher than cell-free or dissolved exposures, which suggests that different absorption and metabolization pathways likely exist [30,122,129]. However, another fact is that the macroinvertebrates that cohabit with cyanobacteria or are long-term/chronically exposed to cyanotoxins show more tolerance to toxicity than those that have not been exposed [47,130].

Although the tolerance and detoxification capacity of benthic macroinvertebrates are still not completely elucidated, several studies into invertebrates and vertebrates tend to relate it to the enzymatic response against cellular oxidative stress or the activating immunity system [32,102,105,129,131]. The role of glutathione (GSH) in MC detoxification has long been known [132], but the effect of antioxidants as blockers of cyanotoxin accumulation and the metabolic pathways involved in detoxification processes have become particularly interesting in the last decade, regardless of antioxidants being produced naturally by the organism or obtained through diet, such as astaxanthins [31,32,133]. However, the detoxification process against cyanotoxins could be more complex, because transcriptomic studies have shown that exposure to these toxins triggers the activation of about 44 immune- and redox-related genes associated with metabolic detoxification phases I and II [32]. Other detoxification ways have also been proposed, such as accelerating intestinal food transit or increasing the bacterial flora that degrades cyanotoxins [31,32]. Although the transfer of toxins between trophic levels in relation to invertebrates is unquestionable [99,101,125], the detoxification capacity observed in freshwater invertebrates is beginning to challenge the established belief that they contribute to the biomagnification of toxins along the food chain [1,29,101]. In fact, even at high concentrations of cyanotoxins, as measured in aquatic consumers of different trophic levels, a meta-analysis based on the biomagnification factor has confirmed biodilution, and not biomagnifications, as the dominant process in aquatic food webs [28,29]. The toxicity transfer of some mayfly species to terrestrial predators, such as bats, has led us to begin taking the aerial phases of hexapods as vectors of toxicity transfer from fresh water to the terrestrial food chain [107,134]. Nevertheless, some stonefly, shore fly and bug adults are capable of eating the cyanobacteria available in terrestrial habitats [83,84,91].

The following Table 1 summarize cyanotoxin producers and main toxins synthesized.

Table 1. Main benthic cyanotoxin producers and main toxic compounds they produce.

Taxa	MCs	ATX	STX	CYN	NODs
Anabaena	[2,19,38,40,41,43,46,135]	[19,22,40,41,43,135]	[1,2,22,38,135]	[19,38,135]	-
Arthrospira	[135]	[135]	-	-	-
Calothrix	[17]	-	-	-	[2]
Cyanomargarita	[136]	-	-	-	-
Cylindrospermum	[19]	[38,135]	[38,137]	-	-
Dactylothamnos	-	-	[136]	-	-
Fischerella	[2,19]	-	-	-	-
Geitlerinema	[2,18,33,38,44,136]	[2,33,38]	[2,38,137]	-	-
Gloeotrichia	[33,38,135]	-	-	-	-
Hapalosiphon	[135]	-	-	-	-
Kamptonema	-	[136]	-	-	-
Leptolyngbya	[18,28,136]	-	-	-	[2]
Lyngbya	[2,17,22]	-	[1,22,38,93,135]	[19,38,93]	-
Microcoleus	[2,17,38,42,46]	[2,28,38,42,46,56,136]	[38,42]	[38,42]	[2]
Microseira	[2]	-	[2]	[2]	-
Nodularia	-	-	-	-	[19,135]
Nostoc	[2,19,33,38,42,93,135]	[38,42]	[42]	[42]	[2,38,135]
Oscillatoria	[1,2,17,18,33,38,42,44,89,93,135]	[19,22,38,42,135,136]	-	[38,42]	-
Phormidium	[2,15–18,33,40,44,51,93,135]	[2,40,56]	[22]	[2]	[2]
Plectonema	[2,135]	-	-	-	-
Pseudanabaena	[33,53]	-	-	-	-
Rivularia	[16–19,33,62,135]	-	-	-	-
Schizothrix	[33]	-	-	-	-
Scytonema	[2,33,38,44]	-	[2,22,38,93,136]	-	-
Tolypothrix	[16,17,39]	-	-	-	-
Trichormus	[38]	-	-	-	-
Tychonema	-	[2,56,136]	-	-	-
Westiellopsis	[2]	-	-	-	-
Wollea	[42]	-	[42]	[42]	-

A compilation of relationships between cyanobacteria and benthic macroinvertebrates is shown in Table S1. Taxon names in the papers are maintained (independently of their validity or update).

3. Conclusions and Future Directions

On the one hand, benthic macroinvertebrates can feed on cyanobacteria, even toxic strains, and are able to survive, grow or complete their life cycle, even by bioaccumulating toxins. On the other hand, the cyanobacteria species or strains that are considered nontoxic can be as harmful to, or are much more harmful than, macroinvertebrates than toxic ones, which suggests that there are other still unknown and potentially toxic compounds. Despite known or unknown toxicity, some macroinvertebrates use cyanobacteria as their main food source, and even choose to live near, on, or in them. Therefore, toxicity should not be the determining factor of the biological relationships between these organisms. The tolerance acquired by benthic macroinvertebrates after millions of years of cohabitation may possibly hold the answer, but the dispersion of currently available data is so wide that it only allows speculation. Perhaps new studies that focus more on the biological synergies of these organisms, rather than on antagonisms, are needed to clear up this mystery.

Exposure of macroinvertebrates to cyanobacteria toxicity can have different short- or long-term effects depending on the way in which it occurs. It has been proven that survival, growth, completing the life cycle, bioaccumulation and behavior can differ if cyanotoxins are obtained through diet or if they are cell-free in water. Toxic effects tend to be generally more lethal or intense with cell-free exposure than when obtained from food. The degree of tolerance might also be responsible for this heterogeneity, and perhaps it can be explained by the existence of different metabolic pathways that manage each exposure type.

Detoxification processes will also be a key factor in macroinvertebrates' response to cyanobacteria toxicity. These processes are being verified in more organisms, with the activation of the main antioxidant enzymes being the focus of attention. However, it is being shown that detoxification may involve a larger number of metabolic processes related not only to antioxidant machinery but also to the immune system itself. This kind of study will be decisive for unraveling what promotes tolerance in benthic macroinvertebrates, especially as it is known in organisms with a close relationship to cyanobacteria, such as those with a mutualistic relationship.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/toxins16040190/s1. Table S1: Compilation of data regarding the relationships between cyanobacteria and benthic macroinvertebrates. References [138–259] are cited in Table S1.

Author Contributions: M.A. was responsible for the ideation; M.A. and N.U.-P. performed the literature search and data analysis and drafted and revised this paper. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The raw data supporting the conclusions of this article will be made available by the author on request.

Acknowledgments: This manuscript was proofread by H&A, Valencia, Spain.

Conflicts of Interest: The authors declare no conflicts of interest.

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