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REVIEW PAPER

Global expansion of toxic and non-toxic cyanobacteria: effect on ecosystem functioning

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Abstract The recent invasion and proliferation of toxic cyanobacteria in diverse aquatic habitats is a well-known worldwide phenomenon. The expansion of cyanobacterial blooms have the potential to significantly alter the structure of the native community and to modify ecosystem functioning. Public and scientific attention was primarily given to the effect on the water quality due to a variety of toxic compounds that some species produce. However, the expansion of toxic and non-toxic cyanobacteria to a wide geographic range may have an impact on the ecosystems, trophic cascades and geochemical cycles. Here we briefly summarize the geographic expansion of cyanobacteria species. We further deliberate the physiological advantages of the invading cyanobacterial species and the ecological effect of cyanotoxins. We discuss recent studies on the contribution of cyanotoxins to the invasion process and the impact toxin producing cyanobacteria have on their newly invaded habitats, the effect of alien cyanobacteria on zooplankton and fish and on the diversity and complexity of the microbial community.

Keywords Cyanobacteria · Cyanotoxins · Aquatic ecosystems · Nostocales · Chroococcales · Invasive species

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Introduction

Cyanobacteria (=Cyanoprokaryota), a diverse group of photosynthetic oxygenic microorganisms, possess cellular mechanisms and acclimation capacity to develop dense populations, frequently referred as "blooms", in lakes, water reservoirs and streams. These features serve many cyanobacteria to expand their distribution as ecological conditions vary due to regional changes in nutrient loads and in biotic setting or due to global climate change. The expansion of cyanobacteria to new habitats was recently discussed in the context of biological invasion of bloom forming species of Nostocales (*Aphanizomenon* and *Cylindrospermopsis*), to temperate freshwater environments (Sukenik et al. 2012; Paerl and Paul 2012) linked global expansion of harmful cyanobacteria to climate change. The invasion and proliferation of cyanobacteria in new habitats may have significant effect on various components of the ecological system from primary producers through to higher trophic levels. Furthermore, toxic cyanobacteria may jeopardize the quality of the aquatic ecosystem and affect various services it provides.

Basic concepts of invasion biology (Vitousek et al. 1997; Ricciardi and Cohen 2007; Pimentel et al. 2001) are insufficient to follow the invasion of cyanobacteria. The invasion of free-living microorganisms to aquatic habitats is rather cryptic and difficult to detect, therefore invasions of these "invisible invaders" have been rarely reported (Litchman 2010). Furthermore, information on prior and current composition of the microbial communities, which is required to determine if a given microorganism is an invader, is often missing. Algae and cyanobacteria are exceptions in that sense as they have a characteristic spectral signature, microscopic morphological features as well as macroscopic visibility producing blooms and scums (Sukenik et al. 2012). However, the invasion of these organisms is frequently reported only at a late stage, as water blooms become visible due to high chlorophyll concentrations, when the invading species has already settled in the receiving waterbody. It is further important to note that in some cases it is still difficult to clearly evaluate if the effects of the increasing development of cyanobacteria is due to a real invasion or to species already present and never recorded or overlooked (Carlton 1996).

Here we briefly summarize the diverse terminology associated with biological invasion and its application to geographic expansion of cyanobacteria species. We further discuss the physiological advantages of the invading cyanobacterial species, the ecological role of cyanotoxins and their contribution to the invasion process and the cyanobacterial impact on their newly invaded habitats. Special attention is given to the effect of alien cyanobacteria on zooplankton and fish community and on the diversity and complexity of the microbial community.

Invasive cyanobacteria—definition and examples

The most common definition of invasive species is "a widespread non-native species that have adverse effects on the invaded habitat" (Colautti and MacIsaac 2004) which was accepted by the International Union for Conservation of Nature. The invasive species become common at places out of their natural range of distribution where they establish, disperse and generate a negative impact on the local ecosystem and native species (Pimentel et al. 2001). Application of this concept to cyanobacterial species or population is rather complicated, as many cyanobacteria species can inhabit an aquatic ecosystem unnoticed, since they may maintain low biomass concentration. Furthermore, the lack of detailed monitoring programs or an insufficiently comprehensive surveillance strategy do not pick up the presence of these species (Kling et al. 2011). Only when a non-native population is widespread, highly abundant and causes ecological or economic harms, it is considered "invasive" (Sukenik et al. 2012).

The invasion of cyanobacteria initiates with dispersion to new zones. It can be expedited by human activities, migrating animals or winds. Aeolian transportation is an efficient means to transfer free-living microorganisms, prokaryotes and protists (Smith et al. 2011). Establishment in an invaded habitat is further supported by a variety of traits that reinforce the proliferation and persistence. Members of the Nostocales order are frequently referred to as invaders. These genera (e.g. *Cylindrospermopsis* and *Aphanizomenon*) include species with different physiological ecotypes growing at different temperatures (Chonudomkul et al. 2004; Üveges et al. 2012) with optimal values between 25 and 30 °C (Padisák 1997; Mehnert et al. 2010; Hadas et al. 2012). *C. raciborskii*, as most Nostocales, have efficient uptake capacities for ammonium (Figueredo et al. 2007) on one hand and can fix atmospheric nitrogen in the absence of combined inorganic sources on the other hand, thus extending the spectrum of ecosystems to which they can invade from eutrophic to oligotrophic environments. They utilize phosphorus efficiently due to their high affinity and high P storage capacity (Istvánovics et al. 2000; Wu et al. 2011) thus, being superior nutrient competitors. Long-term persistence is confirmed by their ability to form dormant cells (akinetes) that may survive long and extreme dispersion routes, on one hand and serve as overwintering forms that survive unfavourable conditions and assure perennial germination and proliferation (Maldener et al. 2014; Cirés et al. 2013). Geographic expansion of Chroococcales is frequently reported as intensive blooms of toxic *Microcystis*. Such events are attributed to global warming and regional eutrophication (Paerl and Otten 2013; O'Neil et al. 2012, see next section). These invading species (Nostocales and Chroococcales) possess additional physiological advantages such as floating and vertical migration capacity to maintain optimal location in the water column, chromatic adaptation to the light field and capacity to screen UV radiation that ensure survival under extreme high light conditions (Paerl and Paul 2012).

Numerous planktonic and benthic cyanobacterial genera produce toxic peptides and alkaloids (Berry et al. 2008; Humpage 2008; Liu and Rein 2010). While the biological role of cyanobacterial toxins is yet to be clarified (Kaplan et al. 2012) evidence is accumulating to indicate their effect on various levels of the ecosystem and their contribution to the invasion process as discussed below.

Factors affecting the spread and growth of cyanobacteria

The factors affecting the distribution and development of cyanobacteria have been the subject of numerous investigations (Paerl and Fulton III 2006; Oliver et al. 2012 and references therein). Eutrophication is considered the main factor promoting the development of selected cyanobacteria in industrialized and developing countries and, more generally, in densely populated areas (O'Neil et al. 2012; Paerl and Paul 2012). The dispersion of toxic cyanobacteria (e.g. *Microcystis*) could be enhanced by global warming (excluding Polar regions where increased temperatures favours Chlorophyta and Bacillariophyta growth), as those species have higher replication rates at high temperatures compared with many other eukaryotic algae, including groups that generally dominate in many freshwater lakes (Paerl and Huisman 2009). De Senerpont Domis et al. (2007) showed an increase in cell replication rate for cyanobacteria but the overall biomass was still well below the diatoms and the chlorophytes. This view has been challenged by Lurling et al. (2013), who demonstrated that the optimum temperature for growth of chlorophytes and cyanobacteria were comparable. These findings do not contravene the important, positive role played by climate warming and higher temperatures on cyanobacteria (Carey et al. 2012; O'Neil et al. 2012). Rigosi et al. (2014) indicated that the relative importance of nutrients and temperature to the promotion of phytoplankton and cyanobacterial biomass in freshwater lakes was dependent on lake trophic state and cyanobacterial taxon. The competitive advantage of selected cyanobacteria is mostly determined by indirect effects of increased water temperatures, which include the increase in the physical stability and reduction of vertical turbulent mixing of the water column, and the extension of the stratification period (e.g. Sommer et al. 2012). Both factors contribute to enhance and extend the period of rapid growth and massive development of blooms (Paerl et al. 2011), although a rapid exhaustion of nutrients can trigger an earlier collapse of the blooming, and a change in ecosystem cycles. Nevertheless, the development and seasonality of cyanobacteria is also strongly influenced by hydrology (hydrological retention time), mixing processes and climatic locations of water bodies (Zohary et al. 2010). Other important factors in the development and dominance of cyanobacteria include the high competition for light and CO_2, the resistance to zooplankton grazing, the ability to accumulate reserves of nutrients and to fix atmospheric nitrogen, and the assimilation of ammonium and competition for trace elements (Hyenstrand et al. 1998).

Overall, from the above considerations, it appears clear how cyanobacteria are able to intrude and colonize every type of terrestrial and aquatic environments. Further, compared with other algal groups, cyanobacteria can take advantage of their tremendous ability to

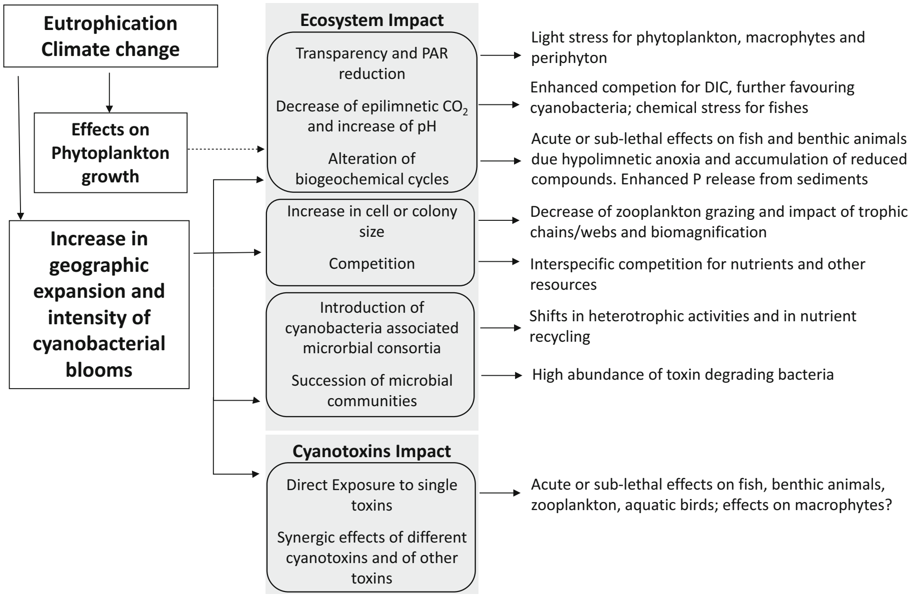

Fig. 1 Schematic presentation of the consequences and impacts of the invasion of toxic cyanobacteria on various components of the aquatic ecosystem

bloom in water bodies rich in nutrients and with stable thermal gradients. In the last decade, the continuous progression of global warming and the increasing contamination of waters due to anthropogenic pollution were the two main elements that favoured the expansion of selected and often invasive cyanobacteria. These two factors, reinforcing each other, could be the cause of a further expansion of cyanobacteria, especially in those countries where the control of nutrient loads is insufficient. The introduction of new species has important implications not only for the contamination of waters used for recreation and drinking purposes, but also for the effects on aquatic biota and ecosystem functioning.

Effects of cyanobacteria on aquatic communities

The excessive growth of cyanobacteria and eukaryotic algae have important consequences on the physical and chemical characteristics of water bodies. Common effects include the decrease of water transparency, the decrease of dissolved dioxide carbon and increase of pH, and the alteration of biogeochemical cycles (Fig. 1). Compared with eukaryotic algae, cyanobacteria have other additional important impacts, which include changes in the biomass size spectrum, biomass edibility and the production of secondary toxic metabolites (Fig. 1).

Competition for resources

If massive, the development of native or invasive cyanobacteria displaces eukaryotic algae with a general decrease of diversity. The effects of the progressive increase of cyanobacteria biomass (e.g. on inorganic carbon speciation, pH, O_2 concentration, light regime and more) are critical for the development of many eukaryotes. Nevertheless, considering the wide acclimation capability and ecological plasticity of cyanobacteria, these changes tend to further reinforce their dominance, especially in enriched environments characterized by wide temporal and vertical fluctuations in resource availability. These aspects have been the object of comprehensive and continuous studies (e.g. Reynolds et al. 2000; Reynolds 2006; Salmaso et al. 2012).

Effects mediated by changes in the physical and chemical environment

The effects on the physical and chemical environment are particularly exacerbated in the case of cyanobacteria, due to their capacity to develop high biomasses in different sites of stratified and mixed lakes (Lindholm et al. 1989). The excessive growth of cyanobacteria can reduce water transparency with light penetration to only few centimetres, and have important effects on pelagic and benthic communities. The reduction of the euphotic zone and especially the excessive increase in the ratio between the epilimnetic mixing layer and the euphotic depth is a detrimental factor for most phytoplankters, but not for species able to control vertical migration, such as many phytoplanktonic cyanobacteria (Mitrovic et al. 2001). It has also been described that under an intense bloom, the cyanobacterial colonies absorb more heat and increase water temperature, thus triggering a higher stability of the water column (Kumagai et al. 2000). During excessive nutrient loads, macrophytes can be severely impacted by low light availability, first shrinking their distribution to shallower areas, and then leaving the place to phytoplankton and cyanobacteria (Scheffer et al. 1997).

In such conditions of persistent turbidity, the nutrient load necessary to recover the lakes to pristine conditions suitable for plant colonisation is lower than that at which they formerly occurred (Havens 2008). These considerations further highlight the difficulty to switch to a previous ecological state when high turbidity associated with excessive development of cyanobacteria and/or other phytoplankters is established.

Implications of a decrease in light availability appear less important for capturing individual food by zooplankton, in which, apart from exceptions (e.g. *Polyphemus pediculus*), vision is not essential to locate prey. Invertebrate predators usually detect prey by sensing the water turbulence originated by swimming or feeding motion (Gliwicz 2004). The decrease of underwater light has direct impacts on the organisms that use the view to search prey or to mate. In fishes, the visual organs are essential for orientation during swimming, to catch prey and avoid predators, and to interact with other individuals of the same species, e.g. in schooling behaviour (Carton 2005; Gray et al. 2014). Though in some species, minimum light intensity thresholds are very low ($<10^{-6}$ lux; Jones et al. 2004), under high turbidity levels the visual systems of fish in any case will be reduced and limited to depths nearer to the surface. Moreover, the increase in turbidity can have differential effects on fishes with different trophic roles. De Robertis et al. (2003) showed that increase in turbidity may be less disadvantageous for planktivorous fish because they will be less susceptible to predation by piscivorous fish, without experiencing a considerable decrease in their ability to capture zooplankton prey. The light field has also an important role on catchability of some species (Buijse et al. 1992), as well as in fish physiology, affecting metabolism, maturation and behaviour.

The high photosynthetic activity following the excessive development of cyanobacteria may produce high amounts of oxygen, accompanied by depletion of CO_2 and increasing pH in the surface waters (Gao et al. 2014; Verspagen et al. 2014). While low carbon dioxide concentrations are a factor of stress for many eukaryotic phytoplankton groups (Salmaso et al. 2015), the CO_2-concentrating mechanism involving active CO_2 uptake and HCO_3^- transport provides significant competitive advantages to cyanobacteria (Shibata et al. 2001; Price et al. 2008).

Optimal pH values for fish growth are between 7 and 9.0, i.e. around the average blood pH (7.4; Wurts and Durborow 1992). If the pH go down below 5 or rises above 10 most fish may become stressed and die. Sub-lethal or lethal high pH values (>10) can be locally reached during intense cyanobacterial blooms and high photosynthetic activity, especially in low alkalinity lakes. These effects are amplified by synergic interactions with other toxicants (e.g. high pH values increase the toxicity of ammonia).

The microbial decomposition of the biomass produced during blooms can severely increase CO_2 and decrease oxygen concentrations and pH in epilimnetic waters especially during night-time. Concurrently, the continuous decomposition of organic matter in the hypolimnion causes oxygen depletion and hypoxia (<2 mg O_2 L^{-1}), or anoxia with production of reduced compounds (ammonia and hydrogen sulfide) and the death of fish, invertebrates and benthic animals (O'Sullivan and Reynolds 2005; Holzner et al. 2009). Low sub-lethal O_2 concentrations severely affect reproductive capacity, behaviour, physiology and expression levels of certain genes directly or indirectly related to cell cycle of fish (Richards and Farrell 2009). Nevertheless, hypoxia tolerance and threshold values are species-specific and can vary enormously. Fishes appear to be less tolerant to low O_2 levels than crustaceans and molluscs (Ekau et al. 2010). In Lake Erie, the increase in cyanobacteria blooms caused extensive hypoxia (Scavia et al. 2014). Under these conditions, Roberts et al. (2009) and Vanderploeg et al. (2009) found that fish avoided hypoxic hypolimnion, while part of the mesozooplankton used the oxygen depleted waters

(1–3 mg O_2 L^{-1}) as a daytime refuge from fish predation, with important implications for food–web interactions and fisheries management.

Effects on trophic webs

The mechanical interference exerted by large cyanobacterial colonies on the grazing activities of non-selective grazers has been widely recognised since the first studies addressing the impact of cyanobacteria on trophic webs (De Bernardi and Giussani 1990 and references therein). At the same time, the experiments and investigations are difficult to generalise, because of the different reaction of various species and strains of zooplankters to the presence of different cyanobacterial colonies (see Kurmayer 2001; Ger et al. 2014). Small-bodied cladocerans are inferior competitors compared with large-cladocerans, which are able to grow and reproduce at lower food levels and to ingest particles of larger size, monopolizing the resources in the absence of fish predation. Conversely, large cladocerans are more susceptible to interference from cyanobacterial filaments, which may cause severe reduction in ingestion rates, while smaller cladocerans can feed between cyanobacterial filaments and large colonies (DeMott et al. 2001; Reynolds 2006). The high upper limit for the spectrum of food particle size allows more filaments to enter the median chamber of large bodied cladocerans, forcing them to clean their food groove more frequently (Gliwicz 2004). Since the fraction of resistant grazing cyanobacteria can increase during eutrophication, this can cause a shift towards a bacteria- and detritus-based trophic web, and therefore a shift towards smaller cladocerans (Ghadouani et al. 2006; Istvánovics 2009).

Cyanobacterial toxins and their effect on the aquatic community

Toxins and toxicity

Toxic cyanobacteria are a major threat to the use of freshwater ecosystems and reservoirs for drinking water, irrigation, and freshwater and marine fishing and recreational purposes (Chorus and Bartram 1999; Carmichael 2001; Osborne et al. 2001). The production of toxins is a distinctive feature largely diffused among cyanobacteria. The number of studies focusing on the effects of cyanotoxins on aquatic organisms increased rapidly during the first half of 2000s (Ibelings and Havens 2008), and particularly during the last 10 years (see general reviews by Ferrão-Filho and Kozlowsky-Suzuki 2011 and Corbel et al. 2014). Over 80 different congeners of microcystins (MC) are known to be synthetized by a wide variety of cyanobacterial genera (Furey et al. 2008; Sarma 2013). MC are hepatotoxic cyclic heptapeptides. Owing to their wide organ targets and effects, the traditional description of MC as hepatotoxins is no longer sufficient to describe their actions in animals (Metcalf and Codd 2012). In addition, a realistic assessment of toxicity effects should take into account the toxicity potential of the more abundant congeners (Wolf and Frank 2002). For example, the toxic equivalent factor (TEF) of MC-LR (the reference and most toxic MC) is equal to 1, while the most abundant MC congener in *Planktothrix* ([D-Asp3] MC-RR) has a TEF 4 times lower than MC-LR. The acute and toxic effects of MC on mammals have also been widely studied, in relation to mass mortality in animals and humans, with acute and chronic exposures to cyanobacterial blooms and toxins, associated several health outcomes, including death (Svirčev et al. 2009; Goudie 2014). Nodularins (NOD) are cyclic pentapeptides that show less structural variability than MC. Many toxicological effects of NOD are similar to those of MC (Metcalf and Codd 2012). NOD production seems restricted to *Nodularia spumigena*. In the recent years, NOD-producing strains of this species made their new appearance in freshwater lakes around Turkey (Akcaalan et al. 2009).

Anatoxin-a (ATX-a), homoanatoxin-a (HTX) and anatoxin-a(S) (ATX-aS) are a group of neurotoxic metabolites produced by a various cyanobacterial species (Méjean et al. 2014; Shams et al. 2014). ATX-a and HTX are nicotinic agonists binding to nicotinic acetylcholine receptors. At high concentrations, these two neurotoxins were identified as responsible for animal mass mortalities (see below). ATX-aS is a naturally occurring organophosphate molecule. ATX-aS irreversibly inhibits acetylcholine esterase in a similar manner as do pesticides and insecticides. Saxitoxins (STX) are a group of neurotoxic alkaloids produced by diverse cyanobacteria but also by marine dinoflagellates. STX interfere with the sodium channels in excitable membranes and can rapidly (minutes) lead to paralysis and death by respiratory arrest (Metcalf and Codd 2012). Cylindrospermopsins (CYN) are alkaloids with multiple organ targets (de la Cruz et al. 2013; Moreira et al. 2013). *Cylindrospermopsis raciborskii* and *Aphanizomenon (=Chrysosporum) ovalisporum*, the main CYN producers, are considered invaders in many water bodies in subtropical and temperate areas (Wiedner et al. 2007; Sukenik et al. 2012; Quesada et al. 2006).

Beta-methylamino-L-alanine (BMAA) is an important neurotoxin (Metcalf and Codd 2012). Although the interest in this toxin remains circumscribed to the possible connections with neurodegenerative disorders caused in humans (Bradley et al. 2013), a number of recent papers also addressed effects caused by BMAA in aquatic biota.

A search on scholarly databases (Nov 2014) indicated that studies focusing on MC are tenfold more numerous than those regarding the other cyanotoxins. However, in the last decade, the increase of papers, which studied CYN and STX was more pronounced. In addition, new secondary metabolites, including new toxins (Jokela et al. 2012; Vestola et al. 2014), continue to be discovered, rendering this research field one of the most active in physiology, food and medical research, as well as ecology (Leão et al. 2012).

Direct exposure of the aquatic biota to cyanotoxins

The impact of cyanobacteria on aquatic biota is mediated by the biosynthesis of toxins that can be released in the environment and ingested by grazers. The introduction in pristine environments of new cyanobacterial species can therefore pose additional stresses and impact to the aquatic biota, with further potential repercussions on their fitness and functionality of trophic webs.

Protozoa

Cyanobacterial secondary metabolites may be toxic to some protists. Urrutia-Cordero et al. (2013) demonstrated that microcystins and others cyanobacterial secondary metabolites may affect protozoa grazing activity. The free-living amoeba *Acanthoamoeba castellanii* responded to some *Microcystis* strains by avoiding grazing reducing growth rate and eventual culture lysis. These effects may have further impact on trophic webs by reducing the recycling of organic matter.

Zooplankton

The intestinal uptake and adverse effects of MC ingested with toxic *Microcystis* strains on unselective filter feeder zooplankton (*Daphnia*) were experimentally studied (Rohrlack et al. 2005). After entering the blood, MC affected the neuromuscular communication, decreasing the beat rates of the thoracic legs, mandibles, second antennae and the activity of the foregut. The death of individuals occurred with an ingestion of 10.2–18.3 ng MC mg^{-1} body fresh weight. The adverse effects of MC on *Daphnia* in laboratory conditions were confirmed by several other studies (e.g. Trubetskova and Haney 2006; Dao et al. 2010). Large filter feeding zooplankters can mitigate the effects of MC through detoxification processes (Monserrat et al. 2003). The enzyme glutathione-S-transferase (GST) is assumed to act as the first step of detoxification in *Daphnia* by conjugating MC-LR with glutathione (GSH). The MC-GSH conjugates are less toxic and excreted more easily. Nevertheless, recent findings provided evidence that GST-mediated conjugation could be of minor relevance for MC tolerance in *Daphnia* in vivo. Sadler and von Elert (2014) showed that the induction of GST activity upon exposure to toxic cyanobacteria was not a specific MC response but a general cyanobacterial effect, suggesting a connection with oxidative stress responses rather than specific detoxification. As highlighted by Sadler and von Elert (2014), further studies are necessary to elucidate the nature of the transport mechanism that efficiently removes unconjugated MC-LR from *Daphnia*. As long as the efficiency of the process is not impaired by excessive concentrations of toxins, detoxification is an important mechanism protecting aquatic biota from toxic effects of MCs. Although accumulation rates and concentrations of MC in large non-selective filter feeders can be very high (up to $>1000\ \mu g\ g^{-1}$ DW; Ferrão-Filho and Kozlowsky-Suzuki 2011), toxins largely accumulate into the body of large zooplankters and not necessarily in the gut and blood (Ibelings and Havens 2008; Shams et al. 2014).

The effects of NOD on zooplankton were documented in the Baltic Sea. The major threats to aquatic communities were considered linked, besides to toxicity of NOD, to the occurrence of a high biomass, oxygen depletion, and reduction in biodiversity (Mazur-Marzec and Plinski 2009).

Individuals of *Daphnia* proved to be influenced also by ATX-aS and STX. De Abreu and Ferrão-Filho (2013) showed effects of an ATX-aS producing *Anabaena spiroides* on the survival and somatic growth of *Daphnia similis*. Ferrão-Filho et al. (2014) showed effects of *C. raciborskii* on the activity of *Daphnia*, with symptoms compatible with the mechanism of action of STX.

Only a limited number of studies have addressed the toxic effects of CYN on invertebrates (Moreira et al. 2013; de la Cruz et al. 2013). Nogueira et al. (2004) showed that *C. raciborskii* strains which produced CYN were more toxic than the non-CYN producers; however, both strains imposed death, suggesting the presence of other toxins or limiting factors in the non-CYN strains. Experiments with *Daphnia* exposed to BMAA showed reduced mobility without acute lethal effects (Lurling et al. 2013).

In nature, intake of cyanotoxins by zooplankton can be controlled by several factors such as food selection, condition of the animals, temperature and selective adaptation of zooplanktonic strains to cyanobacterial toxins (Hairston et al. 2001; Ibelings and Havens 2008; Chislock et al. 2013). These factors, which contribute to avoid, mitigate (or even increase) the effects of MC and other cyanotoxins, could explain the discrepancies in the results obtained in laboratory- and field-based studies. Nevertheless, even focusing exclusively on laboratory studies, the meta-analysis made by Wilson et al. (2006) showed that filamentous cyanobacteria was better food than single-celled cyanobacteria and that the presence or absence of toxic compounds (mostly MC) in the diet had no overall influence on zooplankton growth relative to control diets. Conversely, the survival rates of zooplankton were more negatively affected by toxic than non-toxic cyanobacteria, relative to starvation. Wilson et al. (2006) concluded that the role of cyanobacterial toxins in the determination of food quality may be less important than widely assumed. The successive meta-analyses by Ibelings and Havens (2008) and Tillmanns et al. (2008) showed how the harmful effects of cyanobacteria on zooplankton were very variable, and that the specific effects of cyanotoxins were difficult to evaluate.

Fish

The accumulation and toxicity of cyanotoxins in fish has been the object of numerous studies (Ferrão-Filho and Kozlowsky-Suzuki 2011). The uptake of MC in fish occurs mainly through ingestions, while absorption through the gill epithelium appears of minor importance (Ernst et al. 2006). MC can accumulate in diverse fish organs, including liver, kidney, brain and muscles (e.g. Xie et al. 2005; Chen et al. 2006). MC concentrations frequently found during *Microcystis* bloom can affect early developmental stages of fish with important impacts on several trophic levels (Malbrouck and Kestemont 2006). However, the effects of cyanotoxins on fish are difficult to generalize, due to different experimental settings in the laboratories, in the field, and the difficulty in extrapolating results to natural conditions. For example, the dosing of MC to fish by injection, oral administration or direct exposure in water usually provides very different results (Berry et al. 2009). The limits of studies focusing only on the short-term effects of given cyanotoxins on fish have been discussed in Sotton et al. (2014a).

Analyzing the accumulation of MC in the whitefish (*Coregonus*), Sotton et al. (2014b) found a significant transfer of MC from *Planktothrix rubescens* to herbivorous zooplankton (and partly *Chaoborus*) to fish. Since after analyzing the whitefish gut only a few or no filaments were observed, zooplanktonic herbivores were demonstrated to act as the vectors of MC to whitefish by encapsulating grazed cyanobacteria through their diel vertical migration. These authors estimated that 75 and 21 % of the total MCs in the white fish came from *Chaoborus* larvae and *Daphnia*, respectively. The effects of these accumulations, however, need to be verified. Even if fishes are able to detoxify and excrete ingested MC, therefore limiting their negative effects under bloom conditions (Malbrouck and Kestemont 2006), genotoxicity can occur following the incorporation of toxins (Sotton et al. 2012).

Accumulation of toxins in fish by the ingestion of zooplankton were also documented for nodularins (e.g. Engström-Öst et al. 2002). Investigations on the accumulation and effects of cyanobacterial neurotoxins (ATX, STX and BMAA) and CYN on fish are more scarce (Ferrão-Filho and Kozlowsky-Suzuki 2011; Puerto et al. 2011; Ríos et al. 2014). Osswald et al. (2009) showed that ATX-a was toxic to carp in early stages of development only at very high concentrations, contrarily to cell extracts that were highly toxic, suggesting that other bioactive substances could be responsible for the extracts toxicity. Comparable results were found considering the effects on fish embryos by pure solutions of STX or CYN and crude aqueous extracts of toxin-producing cyanobacteria (Oberemm et al. 1999; Berry et al. 2009). Purdie et al. (2009) described the occurrence of several neuro-muscular and developmental abnormalities in zebrafish induced after BMAA exposure.

Benthic animals, waterfowl and macrophytes

Accumulation and toxic effects of MC and NOD were confirmed in different molluscs and other invertebrates (e.g. Maršálek and Bláha 2004). Gastropods and bivalves can accumulate MC up to 436 $\mu g\ g^{-1}$ DW (Ozawa et al. 2003) and 630 $\mu g\ g^{-1}$ DW (Yokoyama and Park 2003), respectively. Similarly, bivalves and crustaceans were shown to accumulate NOD, CYN, STX (Ferrão-Filho and Kozlowsky-Suzuki 2011), while little is known about ATX.

Mass mortalities of water birds have been linked to the ingestion of organic biomasses contaminated by MC, NOD, CYN, ATX-a, ATX-aS and STX (Stewart et al. 2008). MC, CYN and ATX were shown to represent a potential risk also to aquatic vegetation. Depending on the toxins and concentrations, changes were observed in the intensity of antioxidant and detoxification processes, growth, pigment pattern change and a series of significant ultrastructural alterations (Jiang et al. 2011; de la Cruz et al. 2013; Ha and Pflugmacher 2013). Measurable effects on the vegetation cells were observed starting from MC-LR and ATX concentrations of 0.5 $\mu g\ L^{-1}$ (Jiang et al. 2011; Ha and Pflugmacher 2013).

Allelopathic effects

A few metabolites synthesized and released by cyanobacteria have allelopathic properties that may affect phytoplankton organisms and aquatic plants (Leão et al. 2009). Most of the interactions mediated by the cyanobacterial allelochemicals were studied in laboratory conditions (e.g. Sukenik et al. 2002; Żak et al. 2012; Shao et al. 2013). Nevertheless, their significance at the ecological level and ecosystemic scale will require further detailed studies. On the other side, cyanobacteria appear affected by a variety of compounds produced by diverse aquatic plants. Rojo et al. (2013) demonstrated that a careful selection of charophytes and higher plants could produce more harmful allelopathic effects on filaments of cyanobacteria than on edible chlorophytes.

Effects on bacterio-plankton community and microbiome

The expansion of cyanobacteria to new habitats is potentially linked with the introduction of a heterotrophic bacterial consortia associated with the invading species and uncommon in the invading habitat. Furthermore, locally abundant microbial community could be affected and the structure of the entire microbial population is prone to temporal variations due to the domination of invading cyanobacteria (Fig. 1). It is therefore important to define to what extent the aquatic microbiomes composition is represented by indigenous populations (natives) and by new arrivals that successfully adapted to the presence and bloom of cyanobacteria (Newton et al. 2011). Heterotrophic bacteria are ubiquitous inhabitants of aquatic ecosystems. They benefit from the presence and activity of photosynthetic cells and are key players in the biomass biodegradation and nutrient recycling. The region that extends outward from a photosynthetic cell or a colony of cells in which the growth of heterotrophic bacterial is stimulated by extracellular products of the cells was termed "phycosphere" (Bell and Mitchell 1972). The phycosphere is thus the aquatic analog of the rhizosphere in soil ecosystems and has direct implications for nutrient fluxes to and from algal and cyanobacterial cells. The most advanced studied phycosphere is the one associated with diatoms in marine environments (Amin et al. 2012). Understanding interactions between cyanobacteria and heterotrophic bacteria is of prime importance to decipher nutrient fluxes and biogeochemical cycles during cyanobacterial bloom events. These blooms represent a nutritious niche for associated bacteria. As the intensity of the bloom depends on environmental conditions such as temperature, light, water currents and nutrients availability, the size and composition of the heterotrophic community associated with the bloom can greatly vary (Dziallas and Grossart 2011). Cyanobacterial blooms always accompanied by high total bacterial abundance, indicating that excessive primary production accelerates the growth of heterotrophic bacteria (Wu et al. 2007). High diversity of a microbial community was demonstrated for *Microcystis aeruginosa* biomass isolated from blooms in Lake Taihu, China, using a metagenomic approach. The bacterial sequences were predominantly Alphaproteobacteria with lower abundance of Betaproteobacteria and Gammaproteobacteria. Gene annotations and assignment of clusters of orthologous groups (COGs) to functional categories, indicate that a large number of the predicted genes are involved in metabolic, genetic, and environmental information processes (Li et al. 2011). A detailed field survey on relationships between specific bacterioplankton taxa and phytoplankton communities showed that biomass of cyanobacteria and Bacillariophyta, as well as water temperature, influenced the bacterioplankton community composition in Lake Taihu. *Microcystis* blooms resulted in low bacterial diversity while Bacillariophyta and Cryptophyta blooms led to more diverse bacterioplankton community. Thus, it was concluded that the succession of phytoplankton communities played key roles in shaping bacterioplankton community composition (Niu et al. 2011). The fixation of atmospheric nitrogen by cyanobacteria provides a special niche for epibiont bacteria that efficiently scavenge for accessible fixed nitrogen (Stevenson and Waterbury 2006). Nitrogen translocation from cyanobacteria to epibionts was demonstrated for bloom forming genera within Nostocales including *Cylindrospermopsis*, *Aphanizomenon* and *Nostoc* (Ploug et al. 2010).

While toxic cyanobacteria may have adverse consequences at various trophic levels, the abundance and the activity of specific bloom associated bacteria may control the fate of the toxic compounds via biological degradation (Fig. 1). Biodegradation appeared to be the main fate for most cyanotoxins in aquatic systems and the relative performance of this process would be very site specific and dependent upon local sediment characteristics and microbial activity (Corbel et al. 2014). Laboratory and field studies strongly indicate that, in shallow lakes, natural eliminations of MCs are due to biodegradation (Chen et al. 2008, 2010; Mazur-Marzec et al. 2009). Heterotrophic bacteria that degrade microcystins and cylindrospermopsin have been found in the water column (Cousins et al. 1996; Christoffersen et al. 2002; Mohamed and Alamri 2012) and in sediments (Holst et al. 2003). Aquatic bacteria from the genus *Sphingomonas* (Bourne et al. 1996; Ishii et al. 2004; Manage et al. 2009) and other related genera (Maruyama et al. 2006; Lemes et al. 2008) can degrade MCs. A MC-degrading gene cluster, *mlrA*, *B*, *C* and *D* was identified in these microorganisms, sequenced and a degradation process was proposed (Bourne et al. 2001; Saito et al. 2003; Imanishi et al. 2005).

Biodegradation has also been shown to be an important process for the removal of the cyanotoxin, cylindrospermopsin (CYN), from contaminated water (Chiswell et al. 1999; Senogles and Smith 2002). Wormer et al. (2008) however, could not demonstrate the biodegradation of CYN with bacterial communities from two water bodies in Spain during a period of 40 days. Other study demonstrated that CYN was degraded by an indigenous microbial flora in waters with a history of *Cylindrospermopsis* blooms (Smith et al. 2008). Despite isolation of many bacteria from CYN enriched cultures, only a single isolate (*Delftia* sp.) degraded CYN (Smith 2005). This may explain the persistence of certain cyanotoxins in aquatic ecosystems and enhance the risk presented by the invasion of toxic cyanobacteria to new locations.

Overall perspective

A matter of concern for the invasion and excessive growth of cyanobacteria is the potential bioaccumulation of cyanotoxins in the lake trophic webs. Bioaccumulation is defined as the ratio between the concentrations of a toxin in an aquatic consumer and in its food. The analysis of the existing literature reinforce a diametrical view, supporting biodilution processes, with possibly some exceptions in zooplankton and zooplanktivorous fish (Ibelings and Havens 2008); (Kozlowsky-Suzuki et al. 2012). Although not as efficient, accumulation of toxins in the trophic webs has been widely demonstrated, and new evidences of accumulation have also been collected for new emerging cyanotoxins such as BMAA (Jonasson et al. 2010). New cyanobacterial secondary metabolites are being frequently discovered and these compounds could affect the ecological balance of the original as well as the new ecosystems (Berry et al. 2009).

The efficiency of the transfer along the trophic chain and the ecological impact of cyanotoxins on aquatic biota continues to remain an open issue, especially if the less studied toxins are taken into consideration. Laboratory experiments typically elucidate single mechanisms of action, but in many cases with toxin exposure concentrations and exposure routes that are rarely encountered in nature. Furthermore, the synergistic effect of various toxins needs better understanding and evaluation in natural systems. Food avoidance and selectivity, and detoxification processes can play an important role in the trophic relationships between cyanobacteria and primary consumers, contributing to mitigate the harmful effects of toxins in natural conditions. These processes must be evaluated in the light of adaptive selective forces, acting at the macro- (geological times) and micro-evolutionary scales (years-decades). The first observations by Hairston et al. (2001), suggesting natural selection for grazer resistance to toxic cyanobacteria, were successively confirmed by Sarnelle and Wilson (2005) and Blom et al. (2006). These studies showed that *Daphnia* clones isolated from lakes with high cyanobacterial biomasses (either *Planktothrix rubescens* or *Microcystis aeruginosa*) were genetically adapted and more tolerant to a higher fraction of toxic cyanobacteria in the diet compared to clones isolated from lakes with low cyanobacterial biomasses. These findings have been recently confirmed and extended by Lemaire et al. (2012) who showed how the mortality in short-time exposures of *Daphnia* to *Microcystis* could be explained by genotype × genotype interactions between the two interacting populations, resulting in local coadaptation in a wide geographic mosaic of coevolution and metapopulations. These considerations highlight the intrinsic difficulty to extrapolate studies made under controlled conditions, based on single clones, and outside specific natural contexts. At the same time, these findings confirm the limits of approaches considering the interacting trophic levels as described in terms of species or functional groups and guilds, disregarding the existence of local adapted populations (Salmaso et al. 2015). These aspects are even more important in a perspective of progressive expansion of the geographic range of cyanobacteria, in particular Nostocales (Sukenik et al. 2012).

The introduction of cyanotoxins is only one of the many elements of stress connected with the geographic expansion of cyanobacteria in new aquatic environments (Fig. 1). For example, mass mortality episodes of fish can be connected with lethal or sub-lethal effects of cyanotoxins, but also with other factors, including oxygen deficiency and excessive concentrations of ammonia during cyanobacteria bloom formation and senescence. Zooplankton starvation and decrease can be also the result of food avoidance and impoverishment of food quality when the fraction of cyanobacteria increases. Ultimately, the fitness of aquatic biota depends on the concurrent (antagonistic, additive or synergistic) effects of several stressors (Fig. 1), whose mechanisms remain to be evaluated quantitatively. These aspects still represent a research gap which are beginning to be filled only recently with studies concerning, for example, the interactive effects of NH_3 and MC on cladocerans (Yang et al. 2012) and the effects of mixtures of cyanotoxins on zooplankton (Freitas et al. 2014).

The expansion and proliferation of toxic cyanobacteria in new habitats is accompanied with changes in the microbial community. The information on diversity of the bacterial consortia and their contribution to geochemical processes and degradation of toxins have recently emerged. The application of advanced genetic techniques to study microbial succession in response to toxic blooms will certainly shed light on this dynamic and complex system.

Notably, at the ecosystemic level, clear impacts connected with the new introduction of cyanobacteria can be attributable to changes in the structure of aquatic communities and biodiversity. This change can be observed with an increase in the biomass fraction of cyanobacteria, relative to the other algal groups. These changes are ultimately mediated by the interaction between trophic status and climate change.

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