Chapter 12
Cyanobacteria

Assaf Sukenik, Ora Hadas and Aaron Kaplan

Abstract The routine monitoring program of Lake Kinneret, initiated as early as 1969, revealed the presence of many species of cyanobacteria. However, it was only the first bloom of the nostocalean species *Aphanizomenon ovalisporum* in 1994 that attracted special attention to this important division. This chapter describes the abundance of the most important cyanobacterial species in Lake Kinneret and discusses their physiological and biochemical characteristics. Special attention is given to their unique features that contribute to their proliferation and their impact on the lake's water quality.

Keywords Water quality · Cyanotoxins · Nostocales · *Aphanizomenon* · *Cylindrospermopsis* · Chroococcales · *Microcystis*

12.1 Introduction

The division Cyanobacteria belongs to the kingdom Monera, which, together with the Eubacteria ("true" bacteria) and the Archaeobacteria, makes up the prokaryota (Sukenik et al. 2009b). Like all other prokaryotic organisms, cyanobacteria lack cellular organelles; their DNA lies free in the center of the cell and is not enclosed within a nucleus. Cyanobacteria contain chlorophyll *a* and other photosynthetic pigments, which give them blue-green, often strong colors. They acquire their energy through oxygenic (oxygen evolving) photosynthesis, and thus are often referred to as algae (blue-green algae, cyanophyta), although their prokaryotic characteristics are well defined and differentiate them from eukaryotic algae. Cyanobacteria

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Table 12.1 The most abundant cyanobacteria species in Lake Kinneret and the timing of their appearance

Order	Species	Years of high abundance	Season
Chroococcales			
	Microcystis wesenbergii	1997, 1999–2001	Feb–Apr
	Microcystis botris	2009	Feb–Apr
	Microcystis aeruginosa	1970, 1971, 1974, 1976, 1979, 1983, 1995–2003, 2006, 2009–2010	Feb–Apr
	Chroococcus limneticus	1996–1997	Apr–Jun
	Chroococcus minutus	1978, 1984, 1995, 2001–2003, 2006–2009	Jun–Sep
	Chroococcus turgidis	1975, 1981–1985, 1996, 2000–2001	Sep–Nov
Nostocales			
	Aphanizomenon ovalisporum	1994–1997, 1999–2001, 2001, 2003–2010	Jul–Nov
	Cylindrospermopsis raciborskii	2001, 2003–2006, 2008–2010	Jul–Nov
Pseudanabaenales	*Planktolyngbya limnetica*	1999–2005, 2010	Jul–Nov

Only species with monthly mean areal biomass concentration >5 g w.w. m^{-2} (at least once) are included in the table. Additional cyanobacterial species, not included in the table due to their low contribution to total phytoplankton biomass, are listed in Table 10.1

have relatively simple shapes. These include simple unicells (as in the genera *Synechococcus* and *Chroococcus*), colonies (e.g., *Microcystis*), and filaments, also known as trichomes (e.g., *Oscillatoria, Aphanizomenon*). More complex forms, which are variations of the original simple forms, also occur such as branched filaments (*Calothrix, Fischerella*), filament aggregates (e.g., *Gloeotrichia*), and sheets or mats (*Merismopedia, Hydrococcus*). Some of the filamentous forms evolved to have specialized cells—heterocytes (previously termed heterocysts)—for nitrogen fixation, akinetes as resting stages and motile hormogonia.

This chapter reports on the abundance of various cyanobacterial species in Lake Kinneret over the past 50 years and describes the physiological and biochemical features of the most abundant species and how these features contribute to their proliferation in Lake Kinneret, their role in the ecosystem, and their impact on the lake's water quality.

12.2 The Key Players in Lake Kinneret

The most abundant cyanobacteria in Lake Kinneret belong to two orders: Chroococcales and Nostocales (Table 12.1, see also Sect. 10.1). The dominant species belong to the genera *Microcystis, Aphanizomenon,* and *Cylindrospermopsis*, some of which are known as producers of cyanotoxins (Sect. 33.1) and develop blooms that under certain environmental conditions appear as a thin film on the water surface and in

Fig. 12.1 Floating mats of *Microcystis* in Lake Kinneret. **a** February 2002, Langmuir lines of floating *Microcystis* colonies off shore near Tabgha (original). **b** March 2009, floating scum of *Microcystis* near the northwestern shore (original). **c** February 2010, large patches of floating *Microcystis* mats near Tiberias. (Air photo by Idan Shaked)

extreme cases as thick scums that last several days. Surface mats of *Microcystis* developed in Lake Kinneret on calm days during February and March, when positively buoyant, gas-vesicle-containing *Microcystis* colonies floated to the water surface during the morning hours. The formed thin surface films were pushed by blowing wind and concentrated near shores to form visible scums (Fig. 12.1). The mats were disintegrated by late afternoon, unless the calm conditions persisted. Interestingly, *Microcystis* concentration in the water column during these months was rather low (normally not more than 5 g w.w. m^{-2}), although colonies of variable sizes could be easily observed even by the naked eye.

A study on the genetic diversity of cyanobacterial communities in Lake Kinneret using various molecular techniques revealed the presence of at least 11 different groups of cyanobacteria and significant differences in the cyanobacterial community structure between epilimnetic and hypolimnetic waters. Interestingly, several amplicones showed similarity to sequences from some groups of cyanobacteria so far found in marine habitats (Junier et al. 2007).

While *Microcystis* proliferated and became visible as floating mats or scums, mainly during the winter months (January–April), *Aphanizomenon* and *Cylindrospermopsis* dominated the lake phytoplankton during the summer and autumn. The latter two species never formed scums, although they possess gas vesicles and their concentration in the water column frequently exceeded 10 g w.w. m^{-2} (Hadas et al. 2012). The more homogeneous vertical distribution of Nostocales trichomes in the water column was attributed to low buoyancy potential and high water turbulence imposed by the typical daily afternoon breeze entering the area during the summer and autumn (Berman and Shteinman 1998, Chap. 9).

12.3 Microcystis in Lake Kinneret

The long-term record of Lake Kinneret phytoplankton composition reveals the presence of various *Microcystis* species (*M. aeruginosa, M. botris, M. flos-aquae, M. wesenbergii,* and *M. viridis*; Sect. 10.1). Winter blooms of *Microcystis* spp. were frequently recorded in the 1970s till the mid-1980s and again since 1995 to present

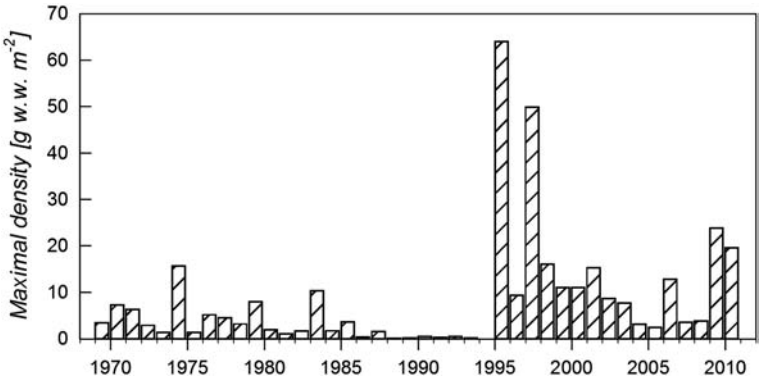

Fig. 12.2 Time series of maximal annual biomass density (g w.w. m^{-2}) of *Microcystis* spp. in Lake Kinneret 1969–2010. (Reproduced with permission from Hadas et al. 2012)

(Fig. 12.2). An exceptional bloom of *Microcystis* sp. was observed in winter 1964 (Pollingher and Kimor 1970; Pollingher 1978) and then once again in 1995. Occasional winter blooms of *Microcystis* sp. (1976, 1978, 1979 and then again in 1995 and 1997) were proposed as the source of disturbance to the annual *Peridinium* spring bloom via allelopathic interactions (Sukenik et al. 2002).

In winter 1995, two *Microcystis* strains (MK-G and MK-B, frequently named also MC-G and MC-B, respectively) were isolated (Hadas unpublished). These strains were clearly distinct from each other by their spectral properties, strain MK-G having a greenish color and strain MK-B a brownish appearance (Masseret and Sukenik 2008), and by the suite of microcystin toxins they produce (Schatz et al. 2005). Furthermore, DNA analysis of 16S rRNA genes of both strains showed high similarity to *M. viridis* or *M. wesenbergii* NIES112 (Schatz et al. 2000).

12.4 The Invasion of Nostocales

The expansion of tropical species of Nostocalean cyanobacteria into lakes in the temperate zone appears to be a worldwide phenomenon (Padisák 1997; Briand et al. 2004; Wiedner et al. 2007; Mehnert et al. 2010; Salmaso et al. 2012; Sukenik et al. 2012a). The invasion was presumably facilitated by human activities or by migrating animals or birds. But reaching a new environment is not sufficient and the invader needs a variety of traits that support its establishment and proliferation. This could be explained by the tolerance of Nostocales to a wide range of environmental conditions and cellular differentiation during their life cycle (Padisak and Reynolds 1998; Vidal and Kruk 2008). One physiological advantage of the Nostocales is their ability to fix atmospheric dinitrogen and thus proliferate in an environment depleted in combined inorganic nitrogen, conditions that prevail in Lake Kinneret during the summer and have become more common since 1994. In addition, Nostocales possess the ability to form dormant cells (akinetes) which stay in the sediment and germinate to produce vegetative cells following improved environmental conditions.

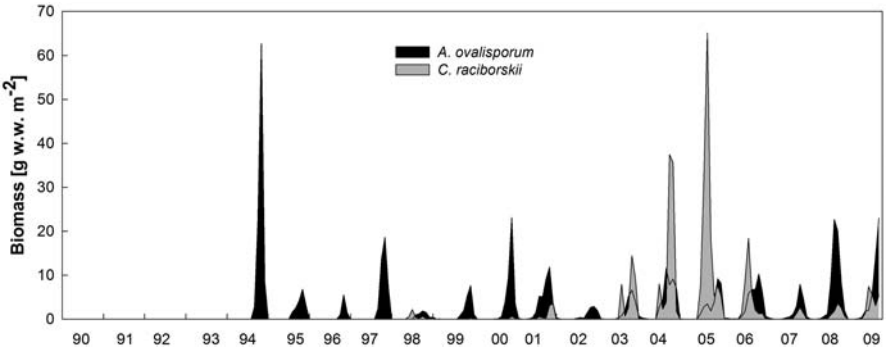

Fig. 12.3 Multi-annual variations in the abundance of two Nostocales species in Lake Kinneret. Note the prompt invasion of *Aphanizomenon ovalisporum* in summer 1994 as compared with a gradual spreading and domination of *Cylindrospermopsis raciborskii*. Data represent monthly average values

The appearance in 1994 and establishment of the Nostocalean species *Aphanizomenon ovalisporum* and *Cylindrospermopsis raciborskii* in Lake Kinneret (Fig. 12.3) could not be advanced without changes in climate conditions such as elevated water temperature, lower summer wind speed, and reduced summer availability of fixed nitrogen (Hadas et al. 2012).

The first appearance of *A. ovalisporum* in Lake Kinneret in August 1994 was apparently boosted by temporary relatively high concentrations of total dissolved phosphorus presumably supported by degradation of the exceptional massive spring bloom of the dinoflagellate *Peridinium gatunense*. In addition, the 1994 bloom was accompanied with exceptionally high alkaline phosphatase (APase) activity (Hadas et al. 1999), which was later attributed to a unique mechanism of phosphate assimilation in *A. ovalisporum* (see below, Bar-Yosef et al. 2010). The N requirement of the summer population of *Aphanizomenon* in1994 was partly provided by nitrogen fixation, as indicated by a high percentage of heterocytes (Pollingher et al. 1998). Since 2001, nitrogen fixation was further demonstrated to take place by *in situ* measurements (Hadas et al. 1999, 2012). For the overall contribution of N_2 fixation by Nostocales to Lake Kinneret's nitrogen balance see Chaps. 19 and 22. The ability of the population to use HCO_3^- as a carbon source under high pH conditions undoubtedly also contributed to its domination (Hadas et al. 1999, as discussed below).

Following the invasion of *A. ovalisporum* in summer 1994, its dormant cells, the akinetes, enabled its establishment as a perennial population. Akinetes were found in the lake's sediments and their distribution in the sediment profile roughly followed the intensity of the bloom in the corresponding year (Ramm et al. 2012; Sukenik et al. 2011). The germination potency of *A. ovalisporum* akinetes and the possible re-proliferation of this cyanobacterium were experimentally demonstrated by incubating lake sediments in nitrogen-depleted BG11 medium, which yielded a dominant population of *A. ovalisporum* (Hadas et al. 1999).

C. raciborskii was first detected in Lake Kinneret in the summer of 1998 and reached a maximum biomass (65 g m^{-2}) in August 2005 (Fig. 12.3), when this sin-

gle species made up 82 % of the phytoplankton biomass. The *C. raciborskii* bloom of summer 2005 collapsed in early September followed by a peak in the *A. ovalisporum* population in November. The long-term record suggests two alternating periods since the 1990s where *A. ovalisporum* dominated the summer–autumn community between 1994 and 2002 and again since 2007, whereas *C. raciborskii* was prominent between 2003 and 2006 (Hadas et al. 2012). The appearance of *A. ovalisporum* and *C. raciborskii* in Lake Kinneret suggests that these species expanded their global distribution as a part of a global invasion process as reported in several lakes in Europe (Sukenik et al. 2012a).

Recently, we reviewed the invasion of Nostocales (cyanobacteria) to subtropical and temperate freshwater lakes and indicated that inappropriate management of watersheds and high pollution triggered the geographic expansion of this group (Sukenik et al. 2012a). But more relevant to Lake Kinneret, these invading species can survive and propagate also under oligotrophic conditions. This is achieved due to their various efficient phosphate acquisition capabilities and nitrogen fixation which seem to be more relevant under oligotrophic than under eutrophic conditions. Thus, in oligotrophic systems, nitrogen cannot be considered as a limiting factor. Phosphate availability controls the development of the N_2-fixing population and its growth. Consequently, management efforts to control eutrophication by reducing N loads, apparently effective in reducing blooms of *Microcystis* and other Chroococcales species, may actually support the growth of Nostocales which easily outcompete native species in such N-limited ecosystems (Schindler et al. 2008).

12.5 Isolation of Toxic and Non-toxic Cyanobacteria Strains from Lake Kinneret

Several species and strains of cyanobacteria were isolated from Lake Kinneret to establish stable cultures of single cyanobacteria species, though none of them was axenic. Two strains of *Microcystis* spp. were isolated, designated MC-G and MC-B, each of which was found to produce different suites of microcystins (see Sect. 24.1) and both lost toxin production capability under laboratory conditions (Schatz et al. 2005). A laboratory culture of *A. ovalisporum* was established from the summer bloom of 1994 (Hadas unpublished). This isolated was identified as a producer of cylindrospermopsin (Banker et al. 1997) and was further studied for its physiological responses to various environmental conditions (Hadas et al. 1999, 2002a). A culture of a non-toxic *C. raciborskii* was established from the 2005 summer bloom (Hadas et al. 2002a) further supporting the reports that the 2005 bloom was non-toxic (Alster et al. 2010). Recently, an additional strain of *A. ovalisporum* and a strain of *Anabaena bergii* were isolated from Lake Kinneret, but neither one was a producer of cylindrospermopsin (Ballot et al. 2011).

Two strains of the pico-planktonic species of the genus *Synechococcus* were isolated from Lake Kinneret and maintained under laboratory conditions (Malinsky-Rushansky et al. 2002). Both strains grew well at high light intensities, but poorly

below 10 μmol photons m^{-2} s^{-1}. Differences in temperature tolerance and photoacclimation suggest that one strain belongs to picocyanobacteria population found in summer below surface waters, while the other stain represents picocyanobacteria found throughout the year at all depths.

12.6 Ecophysiological Properties of Toxic Cyanobacteria from Lake Kinneret

Isolated toxic cyanobacteria species were maintained in laboratory cultures in BG11 medium under continuous low light (10–30 μmol photons m^{-2} s^{-1}). The cultures were studied under controlled environmental conditions to gain a better understanding of the physiological properties that have stimulated their proliferation and bloom formation. The following environmental conditions were examined: temperature, irradiance, phosphate, N:P ratio, $NaHCO_3$, and salinity, indicating that the optimal conditions for *A. ovalisporum* growth under laboratory conditions were close to those observed in the lake in 1994 (Hadas et al. 1999, 2002a, b).

Optimal Light and Temperature for Growth and Photosynthesis– The growth and photosynthetic activity responses of *A. ovalisporum, C. raciborskii,* and *Microcystis* strains (MK-G and MK-B) to different temperatures were studied under laboratory conditions. The optimal temperature for growth varied among these species (Table 12.2). *A. ovalisporum* demonstrated maximal growth rate (0.3 day^{-1}) between 26 and 30 ℃. *Microcystis* strain MK-G demonstrated similarly high growth rates (0.3 day^{-1}) at a wide range of temperatures (20–35 ℃). The MK-B strain had a higher optimal temperature range (30–35 ℃). The optimal temperature for growth of each species or strain verifies its appearance during different seasons in the lake, in agreement with the temperature changes in water column: *A. ovalisporum* and *C. raciborskii* in late summer and autumn, *Microcystis* MK-G (green) in winter and *Microcystis* MK-B (brown) at the beginning of summer.

The saturating light energy for photosynthesis (E_k) was evaluated by running photosynthesis versus irradiance experiments using a photosyntethron, as described by Dubinsky (1980) and Malinsky-Rushansky et al. 2002. All examined strains demonstrated low E_k values (between 12 and 50 μmol photons m^{-2} s^{-1}; Table 12.2), suggesting adaptation to low ambient irradiance. Photoinhibition occurred in *A. ovalisporum* exposed to light intensities higher than 300 μmol photon m^{-2} s^{-1}, but was less obvious in *Microcystis* strains (Hadas et al. 1999, 2002b).

Phosphate Requirement– As in many cyanobacteria, the growth of *A. ovalisporum* was strongly affected by phosphorus availability. In laboratory experiments, maximal growth rate was obtained at inorganic phosphorus (Pi) concentrations above 40 μM. But unlike many members of the Chroococcales, *A. ovalisporum* did not respond to phosphate depletion in the medium by prompt increase in APase activity. This route of phosphate scavenging is efficiently operated only after the internal pool of polyphosphate (polyphosphate bodies, PPB in Fig. 12.4) was utilized. The

Table 12.2 Ecophysiological properties of various cyanobacteria species and strains isolated from Lake Kinneret. (Adopted from Hadas et al. 1999, 2002a, b)

Species	Temperature[a] (℃)	Growth rate (μ) day^{-1}	Light[b] (μmol photons m^{-2} s^{-1})
Aphanizomenon ovalisporum	26–30	0.2–0.3	12–50
Cylindrospermopsis raciborskii	26–32	0.34	12
Microcystis (MK-G)	20–26	0.37	12
Microcystis (MK-B)	30–35	0.26	12–50

[a] Optimal temperature for growth and maximal growth rate
[b] Saturating light for maximal photosynthetic rate

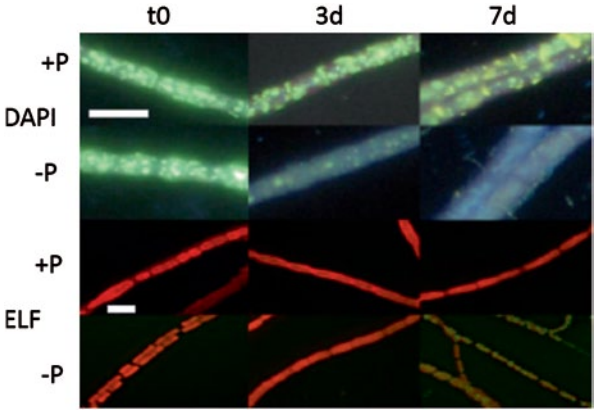

Fig. 12.4 The response of *Aphanizomenon ovalisporum* to inorganic phosphate deprivation is demonstrated by the temporal dynamics in the internal pool of polyphosphate bodies (PPB) and the in situ APase activity in control (+P) and phosphate-deprived (−P) cultures. PPBs are visualized as *greenish granules* using *DAPI* staining, and APase activity is depicted by *green color* using enzyme-labeled fluorescence (*ELF*)–APase protocol (Bar-Yosef et al. 2010). Experimental cultures were sampled at time 0 (*t0*), after 3 (*3d*) and 7 days (*7d*) of growth with or without P. Scale bars indicate 10 μm. (Reproduced with permission from Bar-Yosef et al. 2010)

abundance of PPB in the cells increased fourfold in Pi-rich conditions compared to Pi-limited cultures, but Pi uptake was faster in Pi-depleted compared to Pi-sufficient cells (Hadas et al. 2002a). A unique mechanism of phosphate assimilation was described in *A. ovalisporum* by Bar-Yosef et al (2010). In order to supply its Pi demand, *A. ovalisporum* excretes secondary metabolites, such as the toxic alkaloid cylindrospermopsin, that induce the synthesis and excretion of APase in eukaryotic algae. Pi released by this enzymatic activity is efficiently assimilated by *A. ovalisporum* due to the presence of high efficient Pi transporter (pstS). Only when internal P sources are diminished, the induction of APase occurs in *A. ovalisporum* (Fig. 12.4). This unique mechanism provides an additional advantage to *A. ovalisporum* for its survival and domination in nutrient-depleted environments. During

the course of the 1994 bloom of *A. ovalisporum,* the total dissolved Pi (TDP) level in the epilimnic water column declined from about 0.5 to 0.1 μM (Hadas et al. 1999), suggesting that *A. ovalisporum* may have sequestered significant amounts of the Pi released during the crash of the *Peridinium* bloom. The Pi quota of the natural *A. ovalisporum* population (mainly stored as PPB) declined from 0.21 μmol Pi mg^{-1} dry weight at the beginning of the bloom in July 1994 to 0.08 μmol Pi mg^{-1} dry weight at the peak of the bloom. Therefore, it was suggested that at the beginning of the bloom, growth of *A. ovalisporum* was not Pi-limited, as was also indicated by the relatively low APase activity in *Aphanizomenon* during this time (Bar-Yosef et al. 2012). One month later, at the peak of the bloom, the cells became Pi-limited, as indicated by the significant rise in APase activity (Hadas et al. 1999).

While poly-P granules/bodies of different sizes and shapes are frequently observed in P-replete cultures of *A. ovalisporum*, they were hardly found in mature akinetes. A detailed study of akinete differentiation clearly demonstrated genome multiplication (associated with massive accumulation of nucleic acids) in akinetes. This process is presumably supported by phosphate supplied from inorganic PPB of vegetative cells and was further interpreted in the context of cellular investments for proliferation following long-term dormancy, as the high nucleic acid content would provide the basis for extended survival, rapid resumption of metabolic activity, and cell division upon germination (Sukenik et al. 2009a, 2012b).

Bicarbonate Assimilation and Sodium Requirement– Assimilation numbers as high as 5 μg C μg Chl^{-1} h^{-1} were recorded in Lake Kinneret during the *A. ovalisporum* bloom in late summer and autumn of 1997. These results were verified in laboratory experiments in which the ability of *A. ovalisporum* to acquire bicarbonate was investigated. Maximal photosynthetic rate of 8 μg C μg^{-1} Chl h^{-1} and $K_{1/2}(HCO_3^-)$ of 24 μM were measured at pH 8.2. At pH 7.0, the $K_{1/2}(CO_2)$ was 2.2 and declined to 0.04 μM at pH 9.0. These results strongly indicated that *Aphanizomenon* is a HCO_3^- user and can explain its high photosynthetic rates during the bloom, under high pH and low dissolved CO_2 conditions. Na^+ concentration of about 5 mM was essential for *Aphanizomenon* growth at high pHs, a concentration that is compatible with the values measured in the lake (Hadas et al. 2002a). Na^+ ions are necessary for HCO_3^- uptake by various cyanobacterial species, and the Na^+ concentration required increases with rising pH (Kaplan et al. 1984).

Accessory Pigments– Cyanobacteria maintain relatively higher growth rates than other phytoplankton species under low light conditions. They efficiently acclimate to low light intensities by reorganizing their photosynthetic machinery including chromatic adaptation to different light spectra through their suite of accessory pigments, including phycocyanin and phycoerythrin. Consequently, they may harvest light in the green, yellow, and orange range of the visible light, which is hardly used by other phytoplankton species. Based on the abundance of these accessory pigments, the dominant cyanobacteria species of Lake Kinneret could be divided into two groups: phycoerythrin-less species (*A. ovalisporum, Microcystis* MC-G, and *C. raciborskii*) and phycoerythrin-containing species (*Microcystis* MC-B). Other light-absorbing compounds that are found in cyanobacteria are mycosporin-like

amino acids (MAA). All MAAs absorb UV light that can be destructive to biological molecules (DNA, Proteins, etc). They are effective antioxidants and are able to stabilize free radicals within their ring structure. MAAs were identified in *A. ovalisporum* and *Microcystis* MK-B strains isolated from Lake Kinneret but were not found in *C. raciborskii* and *Microcystis* MK-G.

12.7 Implication of Cyanobacteria to Water Quality and Lake Kinneret Management

It is widely acknowledged that blooms of cyanobacteria in aquatic ecosystems may have impacts on water quality, biological communities, and ecosystem services. Under eutrophic conditions, the potential for cyanobacteria dominance rises rapidly as total phosphorus (TP) increases and the TN:TP ratio decreases (Downing et al. 2001). However, the response pattern in any given system depends also on other factors, such as mean depth, mixing regime, flushing rate, water temperature, wind, and water turbulence. The expansion and establishment of Nostocales as a summer–autumn stable population in Lake Kinneret provides a special example for the hypothesis about cyanobacterial dominance under low N:P ratio (Schindler 2006; Smith 1983). Nostocales appearance was predicted in response to the diminishing dissolved inorganic N (DIN), and the intensity of the bloom was associated with the availability of phosphate (Hadas et al. 2012). It was further suggested that the persistence of the Nostocales population in Lake Kinneret (since 1994) was supported by a combination of their diazotrophic activity and regional climatic and limnological conditions. The latter includes: increased temperatures, changes in wind regime that affect physical mixing processes and water turbulence, and variations in nutrient availability, as well as interactions between various phytoplankton species (Hadas et al. 2012). We doubt whether the winter–spring abundance of *Microcystis* in Lake Kinneret in the past 15–17 years indicates eutrophication of the lake as the monthly averaged density of *Microcystis* exceeded 5 g m^{-2} several times also in the 1970s and 1980s (see 1970–1985 in Fig. 12.1). The exact reasons for the high *Microcystis* biomass in January–March 1995 (~60 g m^{-2}) and in May 1997 (~30 g m^{-2}) are not fully understood. However, we proposed the involvement of allelopathic compounds as mediators that control, among other factors, the abundance and intensity of *Microcystis* populations in Lake Kinneret (Sukenik et al. 2002; Vardi et al. 2002).

Toxin production by certain cyanobacteria (e.g., *A. ovalisporum, C. raciborskii, Microcystis aeruginosa*) may lead to a wide array of biological impacts including: allelopathic effects on other phytoplankton (Sukenik et al. 2002; Leão et al. 2009; Kaplan et al. 2012); suppression of zooplankton grazing leading to reduced growth and reproductive rates and changes in domination (Gilbert 1990; Ghadouani et al. 2004); and hepatotoxic effects on fish (Andersen et al. 1993). Toxins affected survival, growth, and fecundity of snails in laboratory experiments (Gerard and Poullain 2005), and the accumulation of toxins in tissues of freshwater clams has been suggested as a route of toxin transfer to semiaquatic rodents and their preda-

tors (Prepas et al. 1997). In addition to potential toxic effects, cyanobacteria blooms may affect grazing zooplankton by mechanical interference with the filtration apparatus (Gliwicz and Lampert 1990; Hambright et al. 2001) that may indirectly impose changes in zooplankton population structure toward small size species (Havens 2008). Given these biological changes, it is important to consider what effects, if any, frequent or persistent cyanobacterial blooms have on biomass and taxonomic structure of fish. Despite numerous case studies and reports, community-level effects of cyanobacterial blooms are not well understood. Impacts of toxins and changes in food web structure/function in response to cyanobacteria are issues that call for better understanding in the Lake Kinneret ecosystem.

It is expected that bloom events of Nostocales will reoccur in Lake Kinneret in response to management attempts to reduce nutrient loads and forecasting global warming. Further, temperature increase would promote the growth and development of Nostocales species in general. Wiedner et al. (2007) who evaluated a case of an earlier rise in water temperature associated with climate change suggested that earlier warming permits earlier germination of akinetes, thereby shifting the pelagic populations to conditions which advance population establishment and growth. While the possibilities to control and reduce the current trend of global climate change are rather limited, the management of eutrophication processes is feasible. Since a synergistic effect of nutrients and climate was frequently indicated in many sites invaded by Nostocales, it is important that nutrient concentrations in Lake Kinneret be reduced substantially from present values if cyanobacterial dominance is to be controlled. Based on long-term experimental manipulation, Schindler et al. (2008) concluded that N-fixing cyanobacteria cannot be limited by a shortage of dissolved N and instead are competitively favored. Thus, reducing N inputs could actually intensify the dominance of N-fixing cyanobacteria, thus enhancing the expansion of invasive Nostocales. A better approach to control and reduce blooms of Nostocales species and their further expansion in Lake Kinneret is to regulate and reduce external and internal sources of phosphorus, a rather complex task by itself.

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