An overview of the distribution and ecology of the alien cyanobacteria species *Raphidiopsis raciborskii*, *Sphaerospermopsis aphanizomenoides* and *Chrysosporum bergii* in Europe

by

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Abstract

Cyanobacteria can form blooms and pose a threat to the functioning of freshwater ecosystems. Cyanobacterial invasions are expected to increase due to climate change. Alien species cause a decline in biodiversity by displacing native species, lead to extinctions, affect food webs, and produce cyanotoxins which potentially impact the environment and human health. Three species, *Raphidiopsis raciborskii*, *Sphaerospermospis aphanizomenoides* and *Chrysosporum bergii*, are considered non-native to European waters. Recently, they have expanded their native habitats and become established in temperate lakes. In this article, we provide a detailed overview of the countries where they are distributed and the occurrence of the blooms in Europe. We discuss the biotic and abiotic environmental factors that influence their establishment, as well as the characteristics of the species that make them so adaptable in non-native habitats. Understanding the interplay of these factors will allow us to better recognise patterns of invasiveness and predict their future threats to ecosystems.

Key words: non-native species, freshwaters, cyanotoxins, invasion, temperate zone, environmental variables

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1. Introduction

Cyanobacteria are ancient, widespread prokaryotes. They thrive in a variety of environments and form visible blooms in freshwaters that have become increasingly common over the past half century (Huisman et al. 2018, Gaysina et al. 2019). Cyanobacterial blooms reduce water clarity, deplete oxygen, produce harmful cyanotoxins, and disrupt food webs by altering the species composition (Paerl & Huisman 2009, Sanseverino et al. 2017).

Anthropogenic eutrophication and climate change are key factors driving cyanobacterial blooms. Human activities, such as agriculture, can cause nutrient pollution that benefits some alien cyanobacteria in temperate lakes (O'Neil et al. 2012, Paerl et al. 2016). Global temperatures are expected to rise by 4°C by the end of the century (Brown & Caldeira 2017). This will reduce water inflow, increase stratification, change weather patterns, and could extend the bloom period of cyanobacteria in shallow lakes (Paerl & Huisman 2009). These changing conditions are likely to promote the migration and dominance of non-native cyanobacteria, leading to changes in the species composition and concentrations of cyanotoxins (Sukenik et al. 2012, Kokociński et al. 2017a, Ullah et al. 2018). In addition, human activities facilitate the spread of cyanobacteria to new areas. Cyanobacteria can be transferred by shipping or aquaculture, and naturally by birds, rivers, or wind (Curren & Leong 2020). The colonization of new habitats is the first step. If these species become abundant and have economic and ecological impacts, they can be recognized as invasive (Colautti & MacIsaac 2004). The success of biological invasions depends on complex interactions between invasive and native species and the abiotic characteristics of the ecosystem. Cyanobacterial blooms can have significant impacts on aquatic ecosystems and human health, highlighting the need for effective management strategies. Therefore, exploring potential management strategies such as reducing nutrient inputs or implementing targeted control measures for invasive species is crucial.

In recent decades, several tropical/subtropical cyanobacterial species have spread to the temperate freshwaters of higher latitudes and some of them have established themselves in the shallow lakes of Europe (Sukenik et al. 2012). Among them, *Raphidiopsis raciborskii*, *Sphaerospermopsis aphanizomenoides* and *Chrysosporum bergii* are cyanobacteria widely recognised as alien to Europe (Stüken et al. 2006, Kaštovský et al. 2010, Zapomělová et al. 2012). All of these species belong to the Nostocales order, and thus are able to produce resting cells (akinetes), are able to fix atmospheric nitrogen, and have a high affinity for phosphorus, providing strong competitive advantages for their invasion (Sukenik et al. 2012). The competitive advantages of *R. raciborskii* are well documented, while there is increasing evidence of similar patterns in *S. aphanizomenoides* and *C. bergii* (Budzyńska et al. 2019, Kokociński & Soininen 2019, Pagni et al. 2020).

The aim of this study is to provide an overview of the distribution and ecology of three cyanobacteria, *Raphidiopsis raciborskii*, *Sphaerospermopsis aphanizomenoides* and *Chrysosporum bergii*, alien to European phytoplankton communities.

2. Materials and methods

A literature review was conducted to investigate the occurrence and blooms of alien cyanobacteria in various water bodies in Europe, as well as environmental conditions favouring these species distribution and establishment. Records of the cyanobacteria were retrieved from reports in Scopus databases, Google scholar, DAISIE and AlgaeBase using the keywords "*Raphidiopsis raciborskii*", "*Cylindrospermopsis raciborskii*", "*Anabaenopsis raciborskii*", "*Spaherospermopsis aphanizmenonoides*", "*Aphanizomenon aphanizomenoides*", "*Anabaena aphanizomenoides*", "*Chrysosporum bergii*", "*Anabaena bergii*", "*Anabaena bergii* var. *limnetica*", "*Anabaena minderi*", "*Chrysosporum minus*", and "*Anabaena bergii* var. *minor*". The search was delimited to European countries. Published studies that contained only the list of species without information concerning the precise location were excluded from the search to avoid duplication. All reports with unnamed water bodies that were the only records in the country were presented as a single location in the middle of the country. Those records mentioned more than once in different reports were presented as a single record. Records of cyanobacterial presence that did not mention the formation of a bloom were represented as black symbols in three sizes indicating different numbers of water bodies. Symbols representing multiple water bodies were placed in the corresponding geographic location or in the centre of the country if the distribution is widespread. The formation of a bloom was represented by a red symbol. The record was considered a bloom if the biomass of cyanobacteria exceeded 10% of the total phytoplankton biomass or it was named by the authors. Maps were created using the Köppen-Geiger climate type map of Europe (adapted from Peel et al. 2007). Altogether, 307 locations of the studied species are reported in this work, 14 of them being classified as a bloom of the alien species.

3. Changes of taxonomic classification of alien species

Cyanobacterial taxonomy has been revised following the polyphasic approach and reclassified based on the phylogenetic taxonomy. Some species were transferred to newly established genera. Specifically, *Sphaerospermopsis aphanizomenoides* (Forti) Zapomelová at al. was reclassified from *Aphanizomenon aphanizomenoides* (Forti) Horecká, Komárek*, Chrysosporum bergii (Ostenfeld) Zapomelová et al.* – from *Anabaena bergii Ostenfeld*, *Raphidiopsis raciborskii* (Wołoszyńska) Aguilera at al. – from *Cylindrospermopsis raciborskii* (Wołoszyńska) Seenayya, Subba Raju (Zapomělová et al. 2009, 2011, 2012; Aguilera et al. 2018). *Anabaena bergii* var. *limnetica* is currently accepted taxonomically as *Anabaena minderi* because the earlier year of taxa description has priority over the synonym. *Anabaena bergii* var. *minor* Kisselev and *Anabaena bergii* f. *minor* (Kisselev) Elenkin have been currently reclassified to *Chrysosporum minus* (Kisselev) Komárek (Komárek 2012). *Chrysosporum bergii/minor* and *Anabaena minderi* have similar morphology and are often considered closely related taxa or even as the same species (Koreivienė & Kasperovičienė 2011). Therefore, in this review, *Chrysosporum bergii* is discussed under these names. The genus *Chrysosporum* includes another morphologically similar species – *Chrysosporum ovalisporum* (formerly *Aphanizomenon ovalisporum*). Although these closely related species can be distinguished morphologically, misidentification may still occur (Stüken et al. 2009). *C. ovalisporum* occurs in tropical, subtropical, and Mediterranean areas and is not widely distributed in the temperate zone (Cirés & Ballot 2016). This species is not under consideration in this review.

4. Alien species distribution and establishment in Europe

Raphidiopsis raciborskii (Wołoszyńska) Aguilera, Berrendero Gómez, Kaštovský, Echenique & Salerno 2018

Syn.: *Cylindrospermopsis raciborskii* (Wołoszyńska) Seenayya & Subba Raju 1972, *Anabaena raciborskii* Wołoszyńska 1912
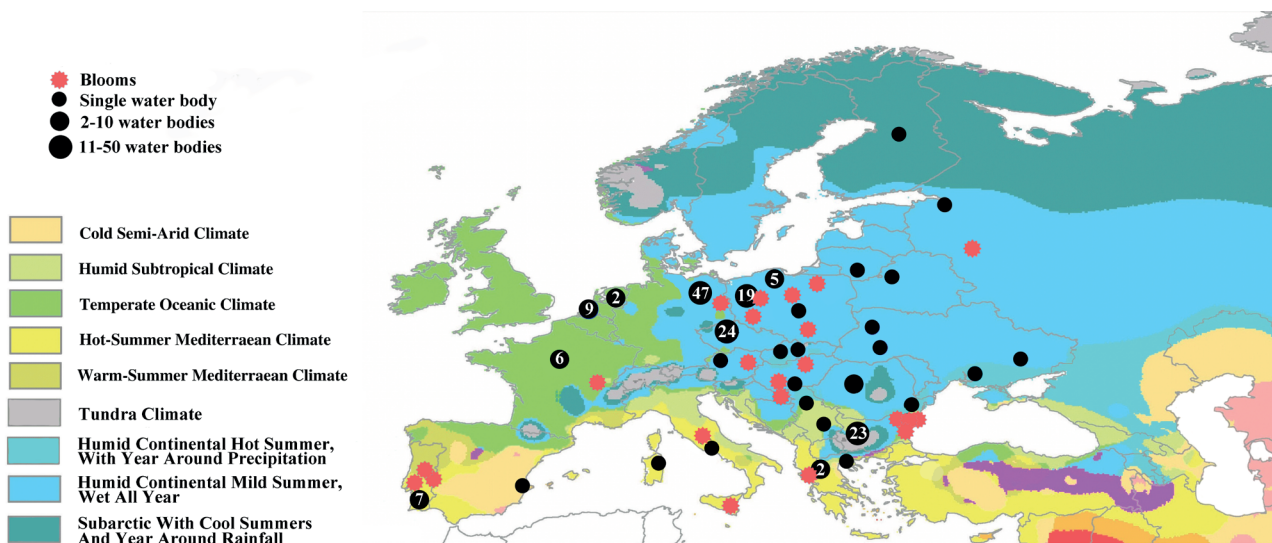
Distribution

Raphidiopsis raciborskii is a globally distributed filamentous diazotrophic cyanobacterium and the most studied invader among cyanobacteria. It was originally described as *Anabaena raciborskii* by Wołoszyńska from Java (Indonesia, 1899-1900). However, polygenetic analyses have suggested central African lakes as the original centre of dispersion (Vico et al. 2020). The species was considered a typical tropical species (Wołoszyńska et al. 1912), but it also occurs in lakes and water reservoirs in the temperate zone, including Europe, where conditions may be different from their previously known habitats (Fastner et al. 2003, Briand et al. 2004, Mankiewicz-Boczek et al. 2012).

According to Padisák (1997), this species was first found in Europe in 1938, in Lake Kastoria in Greece (Fig. 1; Table S1). In the 1960s and 1970s, the species was observed in Belarus (Mikheeva 1967), Ukraine (Hamar 1977, Horecká & Komárek 1979, Présing et al. 1996), Hungary (Padisák 1997 and references therein), Austria (Claus 1961, Padisák 1997 and references therein), Slovakia (Horecká & Komárek 1979) and the Czech Republic (Horecká & Komárek 1979). A sudden increase of new reports in Europe indicated that this was a new invader (Padisák 1997). In 1973, the species was also reported from northern Europe, namely from a highly modified ecosystem – Lake Pątnowskie, a strongly heated lake used for cooling a power plant in Poland (Burchardt 1977), and later in Lake Jieznas in Lithuania in 1988 (Kavaliauskienė 1996). Later still, in the 1990s, *R. raciborskii* was found in the water body near St. Petersburg (Russia) (Balashova et al. 1999), 7 water bodies in Germany (Krienitz & Hegewald 1996, Fastner et al. 2003, Mischke 2003, Nixdorf et al. 2003, Stüken et al. 2006, Botanic Garden & Botanical Museum Berlin 2021), a gravel-pit lake, Janíčkov dvor, in Slovakia (Maršálek et al. 2000), a fishpond, Mézeshegyi-tó, in Hungary (Borics et al. 2000), several water bodies in Romania (Cărăuş 2012), 3 water bodies in France (Coûté, Leitao & Martin 1997, Briand et al. 2002), Lake Volvi and the River Strymon in Greece (Padisák, 1997 and references therein), and 10 water bodies in Portugal (Saker 2004). There was a considerable increase of new reports in the first two decades of the 21st century: in Lake Zazari in Greece (Vardaka et al. 2005), the River Seine and water bodies from Viry-Châtillon, Chanteraînes, Courneuve in France (Druart & Briand 2002; Gugger et al. 2005), Lakes Albano, Trasimeno, Cedrino, and Biviere di Gela in Italy (Manti et al. 2005, Barone et al. 2010), Lake Albufera in Spain (Romo et al. 2008 and references therein), 41 lakes in the Berlin-Brandenburg region in Germany (Stüken et al. 2006, Haande et al. 2008, Botanic Garden & Botanical Museum Berlin 2018), at least 24 new localities in Poland (Stefaniak & Kokociński 2005, Kokociński et al. 2009, Budzyńska & Gołdyn 2017), Lake

Figure 1

Distribution of the alien *Raphidiopsis raciborskii* in Europe. Updated Köppen-Geiger climate type map of Europe (adapted from Peel et al. 2007).

Sakadaš in Croatia (Mihaljević & Stević 2011), Slatina pond and Reservoir Aleksandrovac in Serbia (Cvijan & Fužinato 2012, Simić et al. 2014), 11 waterbodies in the Netherlands (Knoben & Wal 2020), Reservoir Kasperivtsi and the Rivers Seret, Dnierp and Don (Ukraine) (Tsarenko et al. 2006, Kaštovský et al. 2010 and references therein; Rzymski et al. 2018) and Lake Nero in Russia (Babanazarova et al. 2015). 23 localities were reported in the Czech Republic (Kaštovský et al. 2010) and 22 localities in Bulgaria in 2000-2015 (Stoyneva-Gärtner et al. 2017). According to Komárek (2013), *R. raciborskii* has spread northward to Finland.

Establishment

R. raciborskii has gradually become the dominant species in Lake Balaton, Hungary, causing blooms several times since 1982 with a maximum chlorophyll-α ranging from 70 to 160 µg l⁻¹, and later in 1992 with a biomass up to 870 mg l⁻¹ in a shallow hypertrophic fishpond in Mézeshegyi-tó (Présing et al. 1996, Borics et al. 2000) (Fig. 1, TableS1). During the years 1993 and 1994, *R. raciborskii* was reported in a shallow, wind mixed urban Lake Alte Donau, in Vienna, Austria, where it contributed up to 90% of the total phytoplankton biovolume (Dokulil & Mayer 1996). During the years 1992, 1995 and 1999, this species reached up to 97% of the total phytoplankton biomass in the Danubian wetlands in Bulgaria (Stoyneva 2003). In 1999, the species accounted for more than 99% of the total phytoplankton density in the Francs–Pêcheur pond in France (Briand et al. 2002). In the years from

1994 to 2004, *R. raciborskii* reached more than 10% of the phytoplankton biomass in Lake Kastoria in Greece (Katsiapi et al. 2013). In addition, the seasonal abundance of *R. raciborskii* reached up to 3 x 10⁶ cells ml⁻¹ in Reservoirs Odivelas, Caia, Maranhão (Portugal) in 1999 (Saker et al. 2004). Due to its adaptation to summer temperatures, prolonged water retention, and wide range of nitrogen levels, the species began to dominate in oligohaline Lake Albufera (Spain) from 1998 to 2006 (Romo et al. 2008). In 2004, *R. raciborskii* reached up to 50% of the total phytoplankton biomass in Italian Lake Albano (Messineo et al. 2010) and in the years from 2005 to 2007 a change in phytoplankton composition was observed in the southern Italian Lake Biviere di Gela due to a high abundance of *R. raciborskii*, which dominated the phytoplankton along with *Chrysosporum ovalisporum* and *Pseudoanabaena limnetica* (Barone et al. 2010). According to Barone et al. (2010), the transformation was due to increased air temperature and evapotranspiration, which reduced the water inflow and disrupted the littoral zone of the lake. *R. raciborskii* accounted for 24% of the total phytoplankton biomass in Lake Scharmutzelsee in Germany in 1999 (Nixford et al. 2003). In the years from 2005 to 2007, *R. raciborskii* was found in Reservoir Rusałka in Poland, where it accounted for up to 79.4% of the total phytoplankton biomass (Budzyńska & Gołdyn 2017). In 2008, it was observed in shallow, turbid, eutrophic Polish lakes (Lakes Żabiniec, Szydłowskie, Niepruszewskie, Bnińskie), where the cyanobacterial biomass accounted for up to 13.9% of the total phytoplankton biomass.

Kokociński and Soininen (2012) found that the biomass of *R. raciborskii* was positively correlated with the total nitrogen, total phosphorus, and conductivity, while negatively correlated with the temperature, ammonium, and orthophosphate. In 2014, this species was found in 24 out of 101 investigated lakes in Poland, where it accounted for 0.09%–24.60% of the total phytoplankton biomass (Kokociński et al. 2017b). The first bloom of *R. raciborskii* in Serbia was observed in the eutrophic lowland river Ponjavica in 2008. The species accounted for more than 85% of the total phytoplankton biomass (Karadžić et al. 2013). In 2018, it accounted for 5–25% of the total phytoplankton density in Reservoir Poroy and Lake Uzungeren in Bulgaria (Stefanova et al. 2020).

According to the Köppen-Geiger climate classification system and a historical overview of the distribution of *R. raciborskii* in Europe, the species first colonised ecosystems in the Mediterranean climate (Fig. 1, Table S1) (Padisák 1997, Peel et al. 2007). Already in the 1970s, this species had spread to the northern part of Europe (Russia) (Balashova et al. 1999). Since then, *R. raciborskii* has significantly expanded its range, establishing itself in various climatic zones such as cold semi-arid, humid subtropics, temperate oceanic, and even in the tundra and subarctic zones. Most reports were in the humid continental climate zone in Central Europe. The northermost locations noted so far are in northwestern Russia (Lake Nero, 57°09'09.9"N 39°26'24.1"E) and Finland (unspecified location) (Komárek 2013, Babanazarova et al. 2015). To date, *R. raciborskii* has been most commonly reported from shallow eutrophic lakes, but also occurs in deep lakes, mesotrophic lakes, mountain lakes, artificial reservoirs, fish ponds, marshes, wetlands, rivers, and river deltas in at least 176 water bodies in twenty-one countries in Europe. The species is widely distributed in Portugal, the Netherlands, Poland, Germany, and Bulgaria, although it may be related to intensive research in these countries. *R. raciborskii* is not only a widespread species, but also a bloom forming species. It has produced blooms in 10 countries where it accounted for up to 99% of the total phytoplankton biomass.

Sphaerospermopsis aphanizomenoides (Forti) Zapomelová, Jezberová, Hrouzek, Hisem, Reháková & Komárková 2010

Syn.: *Aphanizomenon aphanizomenoides* (Forti) Hortobágyi & Komárek 1979, *Anabaena aphanizomenoides* Forti 1911, *Aphanizomenon sphaericum* Kisselev 1955

Distribution and establishment

Sphaerospermopsis aphanizomenoides was originally described from Lake Anatolia in Turkey in 1911 (Geitler 1932), but has also been reported from tropical and subtropical regions in Asia (Malaysia, India) and South America (Brazil) (Desikachary 1959; Prowse 1972; see references in Horecká & Komárek 1979; Bittencourt-Oliveira et al. 2011) (Fig. 2; Table S2). In the second half of the 20th century, *S. aphanizomenoides* was found in warmer areas of Europe and from 1950
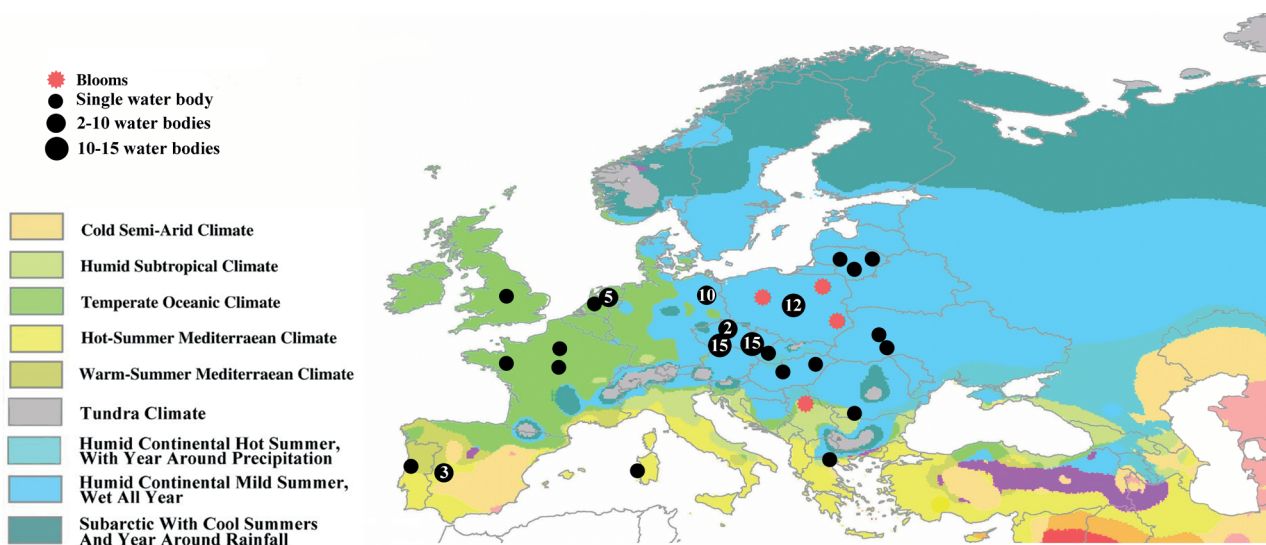

Figure 2

Distribution of the alien *Sphaerospermopsis aphanizomenoides* in Europe. Updated Köppen-Geiger climate type map of Europe (adapted from Peel et al. 2007).

till the first decade of the XXI century has been noted in Hungary (Hortobagyti 1955, Borics et al. 2000), 32 sites in the Czech Republic (Horecká & Komárek 1979, Zapomělová et al. 2012), the Danube River in Romania (Cărăuş 2012), and Lake Stará Morava in Slovakia in 1997 (Hindák 2000). At the beginning of the 21st century, *S. aphanizomenoides* was observed in Lake Vela in Portugal (de Figueiredo et al. 2010), 3 water bodies in France (Brient et al. 2009, Ledreux et al. 2010), Lake Doirani in Greece (Vardaka et al. 2005), a pond in Casas de Millán, and Reservoir Montijo and River Guadiana in Spain (Moreno et al. 2005, Wörmer et al. 2011). In Serbia, this species was first detected in the Ponjavica River in 2002 (Karadžić et al. 2013), and six years later it accounted for 24% of the total phytoplankton biomass (Jovanović et al. 2015). *S. aphanizomenoides* was reported in at least 15 water bodies in Poland and formed blooms in three of them (Reservoir Rusałka, Lakes Swarzędzkie and Uścimowskie) (Stefaniak & Kokociński 2005, Kokociński & Soininen 2012, Budzyńska & Gołdyn 2017, Budzyńska et al. 2019). It also has been found in 10 water bodies in Germany (Stüken et al. 2006), 6 water bodies in the Netherlands (Knoben & Wal 2020), in the United Kingdom (John et al. 2002), the hypereutrophic Cabras lagoon in Italy (Pulina et al. 2011), Reservoir Kasperivtsi and River Seret in Ukraine (Rzymski et al. 2018), and Lakes Jieznas, Gauštvinis and Širvys in Lithuania (Karosienė et al. 2020). It is considered invasive in Spain, Poland, Germany, and the Czech Republic (Stefaniak & Kokociński 2005, Stüken et al. 2006, Kaštovský et al. 2010).

S. aphanizomenoides was originally described from the Mediterranean climate in the Asian part of Turkey (Geitler 1932). While its native habitat is considered to be near the European border, it has recently expanded its distribution in Europe significantly. It has become established in various climatic zones such as the Mediterranean, humid subtropical, and temperate oceanic climates. It has never been found in cold semi-arid, tundra or subarctic climates. Similar to *R. raciborskii*, most reports have been found in the humid continental climate zone in Central Europe. The northernmost location noted so far is in Lithuania (Lake Gauštvinis, 55°38'54.0 "N 23°11'35.6 "E) (Karosienė et al. 2020). In total, the species has been recorded in 15 countries in at least 83 water bodies. It formed blooms in 4 water bodies where it accounted for up to 62% of the total phytoplankton biomass.

This cyanobacterium may be even more common than recorded due to its morphological similarity to the trichomes of *Aphanizomenon gracile* when lacking akinetes (Zapomělová et al. 2012).

Chrysosporum bergii (Ostenfeld) Zapomelová, Skácelová, Pumann, Kopp & Janecek 2012

Syn.: Anabaena bergii Ostenfeld 1908

Distribution and establishment

Chrysosporum bergii and the morphologically similar *Chrysosporum minus* were originally distributed in the habitats of the Aral Sea and the Ponto-Caspian region, which includes the Caspian Sea, Lake Issyk-Kul, the Black Sea, lakes near the Ural Mountains, and relict lakes in Central Asia (Elenkin 1938; Gollerbakh et al. 1953; Proshkina-Lavrenko & Makarova 1968). Several strains are known from Africa and Australia (Stüken et al. 2009; Koreivienė & Kasperovičienė 2011). Both species were found in the brackish Danube delta, which is the oldest record of their occurrence in Europe (Vladimirova & Danilova 1968). Later, they have also been reported from Serbia (Cvijan & Krizmanić 2009; Simić et al. 2014), and the Netherlands (Veen et al. 2015), but the specificities of species are poorly described. Only *Chrysosporum minus* has been described in Austria (Hindák & Deisinger 1989; Hindák 1992). *Chrysosporum bergii* has also been reported from the River Dyje (the Czech Republic) (Heteša et al. 1997), the gravel pit lake near Trávnik (Slovakia) (Hindák 2000), one water body in Belarus (Mikheeva 1999), and more recently in the Marathonas reservoir (Greece) (Katsiapi et al. 2011). This species occurred in 13 out of 142 German water bodies studied in 2004, although *Anabaena bergii* var. *minor* Kiselev and *Anabaena bergii* f. *minor* were considered synonyms to Anabaena bergii Ostenfeld by these authors (Stüken et al. 2006). There are numerous reports describing the occurrence of *C. bergii* in Poland (Kokociński et al. 2013, Budzyńska & Gołdyn 2017, Budzyńska et al. 2019, Kokociński & Soininen 2019). In 2012 *C. bergii* occurred in 7 out of 19 randomly selected lakes in Poland. Therefore, it was considered as a common species in this region, although it has never formed blooms (Kokociński & Soininen 2019). The latest record of this species is from Lake Vaya in Bulgaria, where it was found in 2018 (Stefanova et al. 2020).

Anabaena minderi was first described in the monomictic Lake Greifen and 4 ponds near Zurich in Switzerland (Huber-Pestalozzi 1938, Couté & Preisig 1978) and under the name *Anabaena bergii* var. *limnetica* in the reservoirs of the Seine and Marne rivers in France (Couté & Preisig 1978) (Fig. 3; Table S3). This taxa has been found in the Trávnik gravel pit lake from the Komárno district (Slovakia) (Hindák 2000), Lake Piasecno (Poland) (Bucka & Wilk-Woźniak 2005), Lakes Šmartinski, Pernijško and Grajševsko (Slovenia)
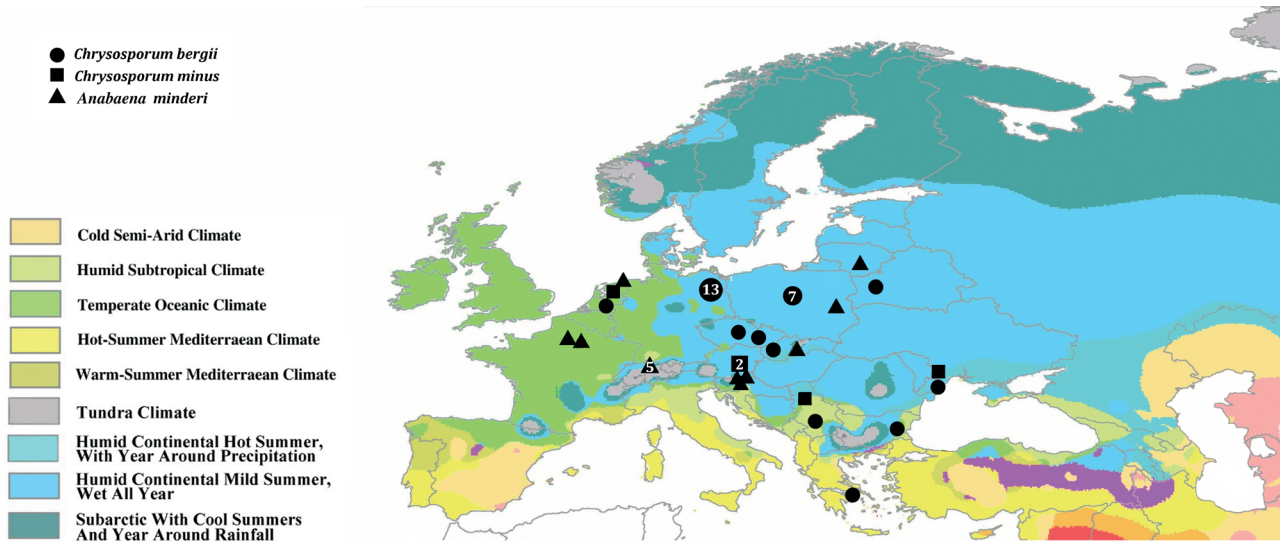
Figure 3

Distribution of the alien *Chrysosporum bergii*, *C. minus* and *Anabaena minderi* in Europe. Updated Köppen-Geiger climate type map of Europe (adapted from Peel et al. 2007).

(Remec-Rekar et al. 2008) and in the Netherlands (Veen et al. 2015). The northernmost locality of *Anabaena minderi* is the most recent record in Europe (Gineitiškės Lake in Lithuania in 2008) (Koreivienė & Kasperovičienė 2011).

Chrysosporum bergii and *Chrysosporum minus* were originally described from the brackish habitats of the Caspian and Aral Seas and tend to invade northern European areas that are less brackish than their original habitats (Zapomelová 2012). In contrast, the morphologically similar *Anabaena minderi* was first described in alpine lakes with low salinity in Switzerland (Huber-Pestalozzi 1938, Komárek 2013). Therefore, probably *A. minderi* should be considered native to European waters. However, its taxonomy is unclear and should be revised. All three species have expanded their distribution into the humid continental climate, as well as temperate oceanic and humid subtropical zones. *A. minderi* occurs also in the tundra climate. The northernmost locations noted so far are in Germany for *C. bergii* (53°10'51.9"N 13°14'33.8"E) (Stüken et al. 2006), in the Netherlands for *C. minus* (unspecified location) (Veen et al. 2015), and in Lithuania for *A. minderi* (Lake Gineitiškės, 54°44'12.4"N 25°11'06.9"E) (Koreivienė & Kasperovičienė 2011). In total, the species have been recorded in 15 countries in at least 29, 5 and 14 water bodies for *C. bergii*, *C. minus* and *A. minderi*, respectively. They have never formed blooms in Europe.

5. Environmental conditions favouring alien species

5.1. Temperature

Temperature is widely considered an important factor for the growth of *R. raciborskii* and its spread. However, both field and laboratory studies show the species can tolerate a wide range of temperatures. A study of 28 mesotrophic and hypereutrophic lakes from tropical, subtropical, and temperate climates reports its presence in lakes with temperatures as low as 11°C (Bonilla et al. 2012). The laboratory experimentation of Briand et al (2004) showed that both tropical and temperate strains were able to grow in a temperature range of 20 to 35°C, with the maximum growth rates at around 30°C. Culture and microcosmos experiments of isolates from water bodies in Germany showed very similar results, with the optimal temperature for this species being around 28°C and the maximum temperature of growth at 35°C. It revealed that *R. raciborskii* had significantly higher growth rates than native species at high temperatures (≥ 20°C), while having lower growth rates at low temperatures (≤ 15°C) (Mehnert et al. 2010). The tolerance of a wide range of temperatures (11 to 35°C) may explain the ability of *R. raciborskii* to establish itself in temperate areas. This species is expected to spread further, and increase its proliferation and competitiveness under global warming scenarios.

The laboratory experiments showed that *S. aphanizomenoides* tolerates a wide range of temperatures (from 10 to 40°C) (Sabour et al. 2009a, Mehnert et al. 2010). However, the maximum growth rates presented in two studies varied: 35°C (Sabour et al. 2009a) and 29°C (Mehnert et al. 2010), probably due to differences in the culturing methods. Even though the species is reported to be able to grow in low temperatures in laboratory conditions, it is only found in the warmest period of the year in the temperate climate, contrary to *R. raciborskii*, reported also form colder months. Similarly to *R. raciborskii, S. aphanizomenoides* is a much better competitor at higher temperatures compared to native species (Mehnert et al. 2010). Savadova et al. (2018) showed that under laboratory conditions *S. aphanizomenoides* was most favoured at temperatures of 20 to 30°C, but the optimal temperatures varied between the strains. A bloom formation of *S. aphanizomenoides* occurred in the small, shallow and eutrophic Ponjavica River in Serbia during warm months of the year. A field study showed the correlation between the species' biomass and high water temperatures (Jovanović et al. 2015). Another field study conducted in a Polish reservoir, reported a bloom of the species in an exceptionally hot summer. According to the authors, the succession of this species was highly dependent on the water temperature (Budzyńska & Gołdyn 2017). Therefore, warming is among the factors promoting this species spread and its establishment in temperate zones.

In contrast to *R. raciborskii* and *S. aphanizomenoides, C. bergii* was a better competitor among nostocalean species at moderate water temperatures (19–20°C) and the maximum temperature for growth of the species was 26.5°C under laboratory conditions (Mehnert et al. 2010). Two field studies conducted in Gineitiškės Lake in Lithuania for *A. bergii* var. *limnetica* and in 19 Polish lakes for *C. bergii* revealed that these species developed in the warmest months, when the water temperature ranged from 20.4 to 23°C and 21.8 to 23.9°C, respectively (Koreivienė & Kasperovičienė 2011, Kokociński et al. 2019). New data from the culture experiment showed that *C. bergii* had its maximum growth rates at 30°C and it decreased at lower temperatures (18–20°C) (Savadova et al. 2018). The variability observed in the results concerning the temperatures associated with the maximum growth rates of *C. bergii* indicates the presence of distinct temperature preferences. This variation could be attributed to the diversity among strains of *C. bergii* or the lack of consensus in the taxonomy of morphologically similar species. Therefore, further studies are needed to clarify the optimal temperature for each species discussed in this paper and to determine whether these species differ in their ecology.

5.2. Illumination

The overview of different culture and field experiments revealed that the optimal intensity for *R. raciborskii* growth varied between 50 and 150 µmol photons m^{-2} s^{-1}, but optimal illumination highly differs among the different strains (Burford et al. 2016 and references therein). This species could grow under low-light conditions (10 µmol photons m^{-2} s^{-1}) in laboratory conditions, therefore, it is considered a shade tolerant species (Pierangelini et al. 2014). Some strains of *R. raciborskii* show photoinhibition under light intensities above 100 m^{-2} s^{-1} (Briand et al. 2004), while another laboratory study reports high growth rates in photon fluxes of 348 µmol photons m^{-2} s^{-1} (Carneiro et al. 2013). The diversity of light preferences may suggest the existence of high- and low-light adapted ecotypes. Furthermore, studies have shown that *R. raciborskii* is shade-tolerant due to its ability to increase the concentration of phycobiliproteins that absorb the broader light spectrum (Pagni et al. 2020).

The light intensity required for the growth of *S. aphanizomenoides* isolates was at moderate light intensities (100–110 µmol photons m^{-2} s^{-1}) (Mehnert et al. 2010). Another laboratory study showed that the photoinhibition of this species is related to water temperature. Growth of *S. aphanizomenoides* at a temperature of 15°C was saturated at a light intensity of up to 130 µmol photons m^{-2} s^{-1}. In contrast, at a temperature of 35°C, the optimal light intensity was reached at up to 442 m^{-2} s^{-1} (Sabour et al. 2009a). Therefore, this species may have a low light preference at low water temperatures. In addition, both *S. aphanizomenoides*, *C. bergii* and *A. bergii* var. *limnetica* were mostly found in water bodies with low transparency (Stüken et al. 2006, Tezanos & Litchman 2009, Budzyńska et al. 2019). These results suggest that all the species mentioned here tolerate low light conditions. This is very beneficial as the blooms themselves decrease the water transparency. Besides this, the cold period and low light intensities are among the most stressful factors for cyanobacterial species inhabiting temperate surface waters (Burford et al. 2016).

The ability to exploit different light conditions is one of the factors contributing to the species succession. Another advantage for the species adaptation is their ability to settle at different depths due to gas vacuoles and to regulate their position in the water column to the most favourable position (Padisák 1997, Antunes et al. 2015).

5.3. Nutrients

Orthophosphate limitation in nature has led to the development of various metabolic strategies that allow cyanobacteria to cope with it. *R. raciborskii* tolerates low environmental phosphorus concentrations due to its high affinity to dissolved inorganic phosphorus (DIP) and its storage capacity (Isvánovics et al. 2000). Thus, the species can store dissolved organic phosphorus (DOP) in the cytoplasm in the form of polyphosphates and utilizes excess internal phosphate under conditions of low DIP in the environment (Burford & Davis 2011). A lake experiment showed that the addition of DIP increased the dominance of this species (Posselt et al. 2009). Therefore, *R. raciborskii* prefers environments with high phosphorus concentrations, but is not dependent on it and can tolerate a wide range of DIP.

S. aphanizomenoides is a highly nutrient-demanding species. The biomass of this species correlated positively with the presence of a high phosphate concentration both in water bodies (Budzyńska et al. 2019) and under laboratory conditions (Savadova-Ratkus et al. 2021). Budzyńska et al. (2019) suggested phosphorus as the primary driving factor of this species growth, and eutrophication as a factor that stimulates the expansion of *S. aphanizomenoides* towards higher latitudes. The species is able to uptake organic phosphorus under phosphorus limited conditions using alkaline phosphatase (Cirés & Ballot 2016). In contrast, the biomass of *C. bergii* correlated negatively with DIP (Kokociński & Soininen 2019). This species occurred more frequently in shallow lakes with low dissolved phosphorus amounts (Kokociński & Soininen 2019).

R. raciborskii dominates in water bodies with different nitrogen concentrations and mostly prefers ammonium as the nitrogen source (Burford & O'donohue 2006, Antunes et al. 2015, Engström-Öst et al. 2015). Energetically, dissolved inorganic nitrogen (DIN) is a more efficient source for *R. raciborskii* growth than atmospheric nitrogen (N_2). For this reason, the uptake rates of DIN are higher than the nitrogen fixation rates. Atmospheric nitrogen fixation gives an advantage that depends on the nitrogen content in the cell (Sprőber et al. 2003).

S. aphanizomenoides is another N_2 fixing cyanobacterium. (Sabour et al. 2009b) found a positive correlation between the species biomass and nitrogen concentration, but nitrogen depletion did not limit the growth of the species. Budzyńska and Gołdyn (2017) showed that the biomass of this species is positively related to high ammonium-nitrogen concentrations. Savadova-Ratkus et al. (2021) observed that inorganic nitrogen significantly affects the growth rate of *S. aphanizomenoides*, but no effect on diazotrophic *C. bergii* was found. Hindák and Hindáková (2001) reported that the occurrence of *C. bergii* and *A. minderi* in Slovak lakes may be related to eutrophication.

The results indicate that *R. raciborskii* is a species tolerant to a wide range of nutrient concentrations. On the other hand, phosphorus concentration is a limiting factor for the growth of *S. apahanizomenoides*. In contrast, nutrients are not among the factors limiting the growth of *C. bergii*, which may even prefer low inorganic phosphorus concentrations.

5.4. Other environmental variables

The concentration of carbon dioxide, pH, and salinity are among the variables important for cyanobacteria proliferation. CO_2 concentration in the water doesn't significantly affect the environmental performance of *R. raciborskii* (Antunes et al. 2015). It can dominate at a pH between 6.9 and 10 (Saker 2004, Antunes et al. 2015), thus, it can tolerate high pH values due to its ability to use carbon sources other than CO_2, which decreases in alkaline environments (Burford et al. 2016). *R. raciborskii* prefers low salinity environments, especially oligohaline and mesohaline conditions (0.5-8 ppm) (Antunes et al. 2015, Engström-Öst et al. 2015). High salinity (> 30 ppm) suppressed growth of this species (Moisander et al. 2012), but at high nutrient concentrations the species was able to dominate even in saline waters (Engström-Öst et al. 2015). *C. bergii* tolerates brackish environments (Zapomělová 2012). The existing literature does not currently include any studies that analyse the potential influence of salinity or pH on *S. aphanizomenoides*.

5.5. Akinetes

The survival of alien species in winter of the colder part of the temperate zone may be explained by the tolerance to low temperatures and the formation of akinetes (resting cells) which are found in most European heterocytous cyanobacterial populations (Padisák 1997, Saker 2004). In contrast, the formation of akinetes in tropical strains is rare. They can persist in the vegetative form throughout the year (Saker & Griffiths 2000). Akinetes formation also promotes survival on dispersal routes (Saker 2004). In Europe, akinetes germination is promoted by warm conditions and therefore high temperatures may enable stronger incoming blooms as a result of higher phosphorus accumulation (Budzyńska & Gołdyn 2017).

5.6. Metabolic plasticity and ecotypes

A great metabolic plasticity or existing ecotypes may explain the success of *R. raciborskii* under various conditions (Briand et al. 2004, Piccini et al. 2011, Bonilla et al. 2012, Kokociński et al. 2017a, Pagni et al. 2020). Metabolic plasticity is a rapid adaptive mechanism under changing environmental conditions since a single genotype can produce different phenotypes by altering its gene expression. Although plasticity is a useful mechanism for becoming established in a new environment, it is energetically disadvantageous. Metabolic plasticity demands energy resources to maintain genetic information, produce the phenotype, acquire information about the environment, and keep the phenotype flexible in relation to the changing environment (Pigliucci 2001). Metabolically plastic species have multiple genes for specific factors; on the contrary, ecotypes of a single species have specific genes for a particular factor and can survive in one type of the environment only due to the presence of these genes. Ecotypes are functionally distinct groups that are genetically and phenotypically stable (Burford et al. 2016; Baxter et al. 2020). Ecotypes differ in their morphology, physiology, toxins, and genetics, and are adapted to local climatic conditions. It is not entirely clear whether the global distribution of *R. raciborskii* is due to high metabolic plasticity, which allows rapid adaptation to different environments, or to the existence of distinct ecotypes that allow to thrive in specific environments (Pagni et al. 2020). Pagni et al. (2020) suggest that distinct ecotypes are the most likely hypothesis, as many studies have confirmed limitations on cyanobacterial growth and development due to genetic differences between strains. Comparison of genetic information of strains isolated from several different ecosystems in a gradient of environmental variables is urgently needed to explain this phenomenon.

5.7. Toxicity

One of the factors influencing the establishment of cyanobacteria in the new aquatic communities is their ability to produce allelochemicals. These allelochemicals influence the phytoplankton's competition, succession, and bloom formation (Fistarol et al. 2004). Alien cyanobacteria can produce potentially harmful compounds, although this ability is strain-specific (Kokociński & Soininen 2012). *R. raciborskii* is known to produce cylindrospermopsin (CYN) and saxitoxin (STX) and its analogues (paralytic shellfish poison, PSP). CYN was first detected in Australia, when it caused an outbreak of hepatoenteritis among indigenous people (Ohtani et al. 1992). Later, CYN production was also observed in New Zealand (Wood & Stirling 2003). STX and PSP, on the other hand, are produced by *R. raciborskii* in South America (Vico et al. 2020).

Contrary to the reports from Australia, Oceania and South America, none of the *R. raciborskii* strains isolated so far from Europe, Africa and North America, has been found to produce known cyanotoxins (Haande et al. 2008, Yilmaz & Phlips 2011, Antunes et al. 2015, Vico et al. 2020). However, some of the *R. raciborskii* strains isolated from Portugal, Hungary, Poland and Germany were demonstrated as toxic to various invertebrate or vertebrate models, even though they did not contain any of the known toxins (Fastner et al. 2003, Saker 2004, Antal et al. 2011, Ács et al. 2013, Poniedziałek et al. 2015). The presence of a specific *cyrJ* gene was detected in a CYN-positive natural bloom sample from a pond in the Czech Republic dominated by both *Raphidiopsis raciborskii* and *R. mediteranea*. However, toxicity was not confirmed in cultures, and the presence of the gene could also be attributed to some native CYN-producing species (Blahova et al. 2021). In addition, microcystin synthetase genes were present in a strain of *R. raciborskii* isolated from Lake Karla (Greece), but toxin production was not confirmed by chemical analyses (Panou et al. 2018).

Synthesis of cyanotoxins depends on environmental variables. The production of CYN by *R. raciborskii* was negatively correlated with temperature. Maximum growth of this species was reached at high temperatures (35°C), while it produced CYN at lower temperatures (20°C), so blooms may have low toxicity at high temperatures (Saker & Griffiths 2000). Therefore, if toxic strains become established in Europe, the colder climate could affect its toxicity. In addition, a positive relationship between light intensity and CYN production was reported by Dyble et al (2006).

Sabour et al. (2005) noted that the strain of *S. aphanizomenoides* isolated from the shallow brackish Lake Oued Mellah in Morocco produced microcystins, but toxicity studies of this species have not been genetically confirmed. *S. aphanizomenoides* has occurred in toxic blooms in Europe, but toxin production by the species has also never been confirmed (Wörmer et al. 2011, Cirés & Ballot 2016, Karosienė et al. 2020). Two nostocalean strains morphologically similar to *Sphaerospermopsis* were positive for *cyrB* and *cyrC* genes, and ESI-LC-MS/MS confirmed CYN production, but phylogenetic analysis of 16S rRNA indicated that they likely belong to a

different genus (Cordeiro et al. 2021).

Chrysosporum bergii was confirmed as a potential CYN producer in Australia (Schembri et al. 2001), but CYN-producing strains of *C. bergii* were reclassified as *C. ovalisporum* in Europe (Stüken et al. 2009). Toxic strains of this species have never been found in Europe.

6. Conclusions

The distribution of three alien cyanobacteria in Europe is increasing. In particular, *Raphidiopsis raciborskii* and *Sphaerospermopsis aphanizomenoides* are apparently able to spread northward from their warm native habitats, and *Chrysosporum bergii* is often found in less brackish environments than in their original localities. There are numerous data describing the wide distribution of *R. raciborskii* in temperate Europe. *S. aphanizomenoides* and *C. bergii* are less prevalent, and knowledge of these species is sparse and sometimes inconsistent.

R. raciborskii is an ecologically adaptable species that tolerates a wide range of temperatures, nutrient concentrations, and illumination, and is therefore able to establish itself in various climates in Europe, from the subtropical to the tundra. In contrast, *S. aphanizomenoides* is a very nutrient demanding species. Some strains of *C. bergii* prefer a low-phosphorus environment and moderate temperatures. Therefore, *S. aphanizomenoides* and *C. bergii* are species with higher demands. However, regarding that the latter two species have spread into Europe more recently, they may develop new adaptive behaviours (acclimatise), dominate, and continue to spread in the coming decades. Temperature increase and eutrophication are the factors that positively affect the geographic expansion and bloom development of *R. raciborskii* and *S. aphanizomenoides*, and they are likely to be further affected as global warming and anthropogenic activities continue. Whether *C. bergii* could begin to form blooms in Europe remains an issue for future studies. There are contradictory reports on the environmental preferences of the three alien species, possibly due to variation among physiologically distinct ecotypes. In addition, the inconsistency of the results on the environmental preferences of *C. bergii* exist due to the lack of agreement in the taxonomy of morphologically similar species. In Europe, the production of microcystins, cylindrospermopsin, anatoxins, saxitoxin or its analogues by the three alien cyanobacteria has never been confirmed. An increasing number of studies prove the production of unknown toxic metabolites by *R. raciborskii*. Some of the species are considered cyanotoxin producers in other continents, and therefore, there is a risk of the dispersion of toxic strains in Europe.

To date, it is not fully understood what are the factors and mechanisms that promote the invasiveness of aquatic cyanobacteria. The establishment of alien species at high latitudes cannot be explained by environmental conditions alone. High adaptability, tolerance to wide ecological ranges, variance of genetic diversity of ecotypes, intraspecific interactions and their role in the trophic food web should be taken into consideration for predicting and understanding the potential success of invasive cyanobacteria in local communities. This would allow us to uncover their dispersal tendencies, toxicity potential and other adaptive behaviours, and predict the ecosystem response to these new inhabitants.

Acknowledgments

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Supplementary materials

Table S1

The recorded localities of *Raphidiopsis raciborskii* in Europe, its climate zones and year of records

Climate zone	Country	Year of record	Water body	Notes	References
Hot-summer Mediterranean climate	Greece	1938	Lake Kastoria	-	Padisák, 1997 and references therein
		-	Lake Volvi and River Strymon	-	Padisák, 1997 and references therein
		1994, 1995, 1999 and 2000	Lakes Kastoria, Volvi, Zazari (eutrophic)	Formed blooms in Lake Kastoria.	Vardaka et al. 2005
		1994-2004	Lake Kastoria (eutrophic)	Formed blooms, maximum biomass - >10 % of total phytoplankton biomass.	Katsiapi et al. 2013
	Portugal	1999	10 water bodies in Portugal	Formed blooms in Reservoirs Odivelas, Caia, Maranhão. Showed toxicity under laboratory conditions.	Saker et al. 2004
	Italy	2002	Lakes Albano, Trasimeno and Cedrino	-	Manti et al. 2005
		2003-2007	Lake Albano	Formed blooms, maximum biomass - 50% of the total phytoplankton biomass.	Messineo et al. 2010
		2005-2007	Lake Biviere di Gela	Formed blooms.	Barone et al. 2010
Cold semi-arid climate	Spain	1998-2006	Lake Albufera	-	Romo et al., 2008 and references therein
Humid subtropical climate	Serbia	2006	Pond Slatina (salt marsh)	-	Cvijan & Fužinato 2012
		2011	Reservoir Aleksandrovac	-	Simić et al. 2014
Temperate oceanic climate	France	1994	2 ponds in Paris area	-	Coûté, Leitao & Martin 1997
		1998 and 1999	Pond Francs–Pêcheur	Formed blooms, more than 99% of the total phytoplankton biomass.	Briand et al. 2002
		-	Water bodies in Viry-Châtillon, Chanteraînes and Courneuve	Strains from Paris Museum culture collection.	Gugger et al. 2005
		2001	River Seine	-	Druart & Briand 2002
	Netherlands	2000, 2001, 2002, 2007, 2008, 2009, 2010, 2011	11 water bodies in the Netherlands	-	Knoben & Wal 2020
Humid continental mild summer, wet all year	Poland	1973	Lake Pątnowskie	-	Burchardt 1977
		-	Several shallow hypertrophic lakes in Wielkopolska region	-	Stefaniak & Kokociński 2005
		2006 and 2007	Lakes Bnińskie, Bytyńskie and Lubosińskie	-	Kokociński et al. 2009
		2005-2007	Reservoir Rusałka	Formed blooms, maximum biomass - 79.4% of the total phytoplankton biomass.	Budzyńska & Gołdyn 2017
		2008	20 lakes in Poznan and Zielona Gora districts	Formed blooms in Lakes Żabiniec, Szydłowskie, Niepruszewskie, Bnińskie, maximum biomass - 13.9% of the total phytoplankton biomass.	Kokociński & Soininen 2012
		2014	24 lakes in Poland	Formed blooms, maximum biomass - 24.60% of the total phytoplankton biomass.	Kokociński et al. 2017b
	Hungary	1970s	Lake Szelidi-tó	-	Padisák 1997 and references therein
		1978	Lake Balaton	Formed blooms.	Présing et al. 1996
		1992-1995	Shallow hypertrophic fishpond in Mézeshegyi-tó	Formed blooms.	Borics et al. 2000
	Romania	-	Several water bodies in Romania	-	Cărăuş 2012
	the Czech Republic	-	Gravel-pit Lakein Chomutov	-	Horecka & Komarek 1979
		-	23 waterbodies in the Czech Republic	-	Kaštovský et al. 2010
	Slovakia	-	Reservoir Boryčki	-	Horecká & Komárek 1979
		1995	Gravel-pit Lake Janíčkov dvor	-	Maršálek et al. 2000
	Austria	-	Water body in Salzlackengebiet	-	Claus 1961
		1979		-	Padisák 1997 and references therein
		1993 and 1994	Lake Alte Donau	Formed blooms, maximum biomass - 90% of the total phytoplankton biomass.	Dokulil & Mayer 1996
	Germany	1990	Lake Lieps	-	Krienitz & Hegewald 1996
		1995 and 2001	Lakes Falkenhagener, Neuer Falkenhagener, Schwielochsee and Kleiner Schwielochsee	-	Botanic Garden & Botanical Museum Berlin 2021
		1999	Lake Scharmutzelsee	Formed blooms, maximum biomass - 24% of the total phytoplankton biomass.	Nixdorf et al. 2003
		1999 and 2000	Lakes Melangsee and Langer See	Showed toxicity under laboratory conditions.	Fastner et al. 2003; Mischke 2003
		-	Lake Zierker See	-	Haande et al. 2008
		2004	39 lakes in the northeast Germany	-	Stüken et al. 2006
		2009	Lake Eichenteich	-	Botanic Garden & Botanical Museum Berlin 2018
	Lithuania	1988	Lake Jieznas	-	Kavaliauskienė 1996
	Belarus	-	-	-	Mikheeva 1967
	Russia	-	Water body in St. Petersburg	-	Balashova et al. 1999
		2010	Lake Nero	Formed blooms, maximum biomass - 23.3% of the total phytoplankton biomass	Babanazarova et al. 2015
	Croatia	2003	Lake Sakadaš	Formed blooms, maximum biomass - 91.4 mg/l.	Mihaljević & Stević 2011
	Ukraine	late 1960s	Water bodies in the region of Pannonia	-	Hamar 1977; Horecká & Komárek 1979
		-	Dniepr River	-	Tsarenko et al. 2006
		2017	Reservoir Kasperivtsi and River Seret	-	Rzymski et al. 2018
Humid continental hot summers with year round precipitation	ukraine	-	Don River	-	Kaštovský et al. 2010 and references therein
	Romania	-	Brakish Danube delta	-	Cărăuş 2012
Subarctic with cool summers and year round rainfall	Finland	-	-	-	Komárek 2013
Humid subtropical climate/ humid continental mild summer, subarctic with cool summers and year round rainfall/tundra climate	Bulgaria	1992, 1995 and 1999	Danubian wetlands (Srebarna, Shabla)	Formed blooms, maximum biomass - 97% of the total phytoplankton biomass.	Stoyneva 2003
		2000-2015	23 lakes in Bulgaria	-	Stoyneva-Gärtner et al. 2017
		2018	Reservoir Poroy and Lake Uzungeren	Formed blooms, maximum biomass - 25% of the total phytoplancton biomass.	Stefanova et al. 2020

Blooms – *R. raciborskii* was considered to have formed a bloom when its biomass exceeded 10% of the total phytoplankton biomass or it was named as such by authors

The recorded localities of *Sphaerospermospsis aphanizomenoides* in Europe, its climate zones and year of records

Climate zone	Country	Year of record	Water body	Notes	References
Hot-summer mediterranean climate	spain	-	Pond in Casas de Millán	-	Wörmer et al. 2011
		2002	Reservoir Montijo and River Guadiana	-	Moreno et al. 2005
	Italy	2007-2009	Hypereutrophic Cabras lagoon	-	Pulina et al. 2011
Warm-summer mediterranean climate	Portugal	2006	Lake Vela	-	de Figueiredo et al. 2010
Humid subtropical climate	Romania	-	Danube River: Upstream confluence with Jiu River	-	Cărăuş 2012
	Serbia	2002	River Ponjavica	-	Karadžić et al. 2013
		2008		Formed blooms, maximum biomass - 24% of the total phytoplankton biomass.	Jovanović et al. 2015
Humid continental mild summer, wet all year	Hungary	1955	Water body near Dabas	-	Hortobagyti 1955
		1992-1995	Shallow hypertrophic fishpond in Mézeshegyi-tó	-	Borics et al. 2000
	The Czech Republic	-	Lake from Moravia	-	Horecká & Komárek 1979
		2004 and 2009	15 localities in South and 2 localities in Central Bohemia and 15 localities in South Moravia	-	Zapomělová et al. 2012
	Slovakia	1997	Lake Stará Morava in Bratislava (eutrophic)	-	Hindák 2000
	Poland	-	Lake/s in the Wielkopolska region	-	Stefaniak & Kokociński 2005
		2006 and 2007	Reservoir Bnińskie	-	Kokociński et al. 2009
		2005-2007	Rusałka reservoir	Formed blooms, maximum biomass - 62% of the total phytoplankton biomass.	Budzyńska & Gołdyn 2017
		2008 and 2009	Lake/s in Poznan and Zielona Gora districts	-	Kokociński & Soininen 2012
		2015	13 lakes in Poland	Formed blooms in Lakes Swarzędzkie and Uścimowskie	Budzyńska et al., 2019
	Germany	2004	10 waterbodies in northeast Germany	-	Stüken et al. 2006
	Lithuania	2014-2015	Lakes Jieznas, Gauštvinis, Širvys	-	Karosienė et al. 2020
	Ukraine	2017	Reservoir Kasperivtsi and River Seret	-	Rzymski et al. 2018
Subarctic with cool summers and year round rainfall	greece	1994, 1995, 1999 and 2000	Lake Doirani	-	Vardaka et al. 2005
Temperate oceanic climate	france	2006	Recreational water bodies in Apigné and Chevreux	-	Brient et al. 2009
		2008	Water body Champs-sur-Marne	-	Ledreux et al. 2010
	The Netherlands	-	Kinselmeer	-	Janse et al. 2005
		2004, 2006, 2007, 2008,2009,2010	Water bodies Paterswoldsemeer, Slotermeer, Zuidlaardermeer and 2 water bodies in Rotterdam and Amsterdam	-	Knoben & Wal 2020
	Great Britain	-	-	-	John et al. 2002

Blooms – *Sphaerospermospsis aphanizomenoides* was considered to have formed a bloom when its biomass exceeded 10% of the total phytoplankton biomass or it was named as such by authors

The recorded localities of *Chrysosporum, C. minus* and *Anabaena minderi* in Europe, its climate zones and year of records

Climate zone	Country	Year of record	Water body	Notes	References
Crysosporum bergii (Ostenfeld) *Zapomelová 2012* (syn. *A. bergii*)					
Humid continental mild summer, wet all year	Slovakia	2000	Gravel pit lake at Trávnik, Štrkovec	-	Hindák 2000
	The Czech Republic	-	Košarska and Stulikova pool in Dyje river	-	Heteša et al. 1997
	Ukraine	-	Brakish Danube delta	-	Vladimirova & Danilova 1968
	Germany	2004	13 waterbodies in northeast Germany	-	Stüken et al. 2006
	Poland	-	-	-	Kokociński et al. 2013
		2005-2007	Rusałka reservoir	-	Budzyńska & Gołdyn 2017
		2015	-	-	Budzyńska & 2019
		2012 and 2013	7 lakes in Poland	-	Kokociński & Soininen 2019
	Belarus	1999	Lake	-	Mikheeva 1999
Temperate oceanic climate	netherlands	-	-	-	Veen et al. 2015
Humid subtropical climate	Serbia	2011	Lake Aleksandrovac	-	Simić et al. 2014
	Bulgaria	2018	Lake Vaya	-	Stefanova et al. 2020
Hot-summer mediterranean climate	Greece	2007	Marathonas Reservoir	-	Katsiapi et al. 2011
Chrysosporum minus (Kisselev) Komárek 2012 (syn. *A. bergii var. minor* Kisselev 1927 and *A. bergii f. minor* (Kisselev) Elenkin)					
Humid continental mild summer, wet all year	Ukraine	-	Brakish Danube delta	-	Vladimirova & Danilova 1968
	Austria	-	Lakes Keutschacher and Hafnerse	-	Hindák & Deisinger 1989
Temperate oceanic climate	Netherlands	-	-	-	Veen et al. 2015
Humid subtropical climate	serbia	2006	Slatina pond (salt marsh)	-	Cvijan & Krizmanić 2009
Anabaena minderi Huber-Pestalozzi 1938 (syn. *Anabaena bergii* var. limnetica Couté et Preisig 1978)					
Humid continental mild summer, wet all year	Slovenia	-	Lakes Pernijško, Grajševsko	-	Remec-Rekar et al. 2008
	Slovakia	1999	Gravel-pit Lake at Trávnik	-	Hindák 2000
	Poland	1999-2000	Lake Piaseczno	-	Bucka & Wilk-Woźniak 2005
	Lithuania	2008	Lake Gineitiškės	-	Koreivienė & Kasperovičienė 2011
Subarctic with cool summers and year round rainfall	slovenia	-	Lake Šmartinski	-	Remec-Rekar et al. 2008
Tundra climate	switzerland	-	Lake Greifen	-	Huber-Pestalozzi 1938
		-	4 ponds near Zurich	-	Couté & Preisig 1978
Temperate oceanic climate	netherlands	-	-	-	Veen et al. 2015
Temperate oceanic climate	france	-	Barrage lakes of the rivers Seine and Marne	-	Couté & Preisig 1978

Blooms – *C. bergii* was considered to have formed a bloom when its biomass exceeded 10% of the total phytoplankton biomass or it was named as such by authors