

4. Geographic distribution of freshwater blue-green algae

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Abstract

The analysis of the currently available data for morphologically unambiguously defined freshwater blue-green algae indicates that besides (sub-)cosmopolitan species, taxa with a more restricted distribution also exist. Many of these have a holarctic or pantropic distribution. It is hypothesized that, besides the distribution of ecological niches, temperature is one of the main controlling factors restricting species to particular latitudinal zones. Furthermore, the presence of species with a regional distribution (endemics) can not be ruled out, indicating that other factors must be considered. The possible role of dispersal capacities and of dispersal rates in relation to the earth history and to the speciation of blue-green algae is discussed.

Introduction

For many groups of microalgae, our knowledge about species distribution and about the factors which govern their distribution is still fragmentary. The main reasons for this situation are, on one hand, the lack of floristic lists for many regions of the world, and, on the other hand, the low level of taxonomic knowledge in many groups. This note analyses the present knowledge about the biogeography of freshwater blue-green algae (cyanobacteria).

Methodological considerations

The study of the distribution of freshwater blue-green algae is hampered by difficulties in describing and recognizing the different taxa due to their often simple morphology. For the identification of freshwater blue-green algae, Geitler's monograph (1932) still remains the main reference, for temperate as well as for tropical regions; however, it mainly deals with species from temperate regions (especially Europe). Specimens collected in the tropics which could not be identified according to the traditional keys were thus often referred to the closest described species from temperate regions. However, the detailed morphological and eco-

logical study of tropical specimens often leads to the recognition of these apparently cosmopolitan species as separate taxa (e.g. Frémy, 1930; Geitler & Ruttner, 1935; Komárek, 1985). Many records in lists from tropical regions thus require careful checking.

Problems in the delimitation of the taxa are further complicated by the use of two widely different taxonomic systems. Drouet's system (summarized in Drouet, 1981) led to the recognition of only 62 taxa and it was followed by several authors for regional floristic studies (e.g. Brannon 1952; Nielsen & Madsen 1948; Zaneveld 1988). However, several experimental studies (e.g. Stam & Holleman, 1979; Stulp & Stam, 1984; Waterbury & Stanier, 1978) have shown that this approach does not reflect the biodiversity of blue-green algae. For the discussions in this paper, only publications following the classical approach were thus taken into consideration. In this system, species can be defined as a complex of natural populations with an overall morphological and cytological similarity and which occupy the same ecological niche (Anagnostidis & Komárek, 1985; Geitler, 1932).

Another problem comes from the fact that no floristic lists exist for many parts of the world (large areas of Africa, Asia, S America, Australia) or that only local collections are available, so that endemic taxa or cosmopolitan forms of low abundance may be over-

looked. The floras of other regions, i.e. Europe and North America, are better documented. Gaps in the knowledge of the distribution of freshwater blue-green algae may also come from an underrepresentation of sampling of certain niches in which blue-green algae are often important. In tropical regions, few data are available for benthic habitats (epilithic and epiphytic blue-green algae), whereas relatively many data exist for the plankton. Benthic habitats seem, however, to harbour a high diversity of forms (especially within the Chroococcales and the Stigonematales).

To discuss the distribution of freshwater blue-green algae in the present paper, only reports of morphologically and ecologically well defined taxa (within the traditional system updated by Anagnostidis & Komárek, 1985) which can hardly be mistaken for others were taken into account. It is reasonable to admit that these data concern populations belonging to the same species. Experimental studies in the genus *Anabaena* s.l. showed indeed that, at least for morphologically complex groups, populations with an identical morphology are also genotypically similar (Stulp & Stam, 1984).

Distribution patterns

Because blue-green algae are an evolutionary very old group, they were often thought to have a cosmopolitan distribution (e.g. Fogg et al., 1973). Due to the lack of sampling in many regions, the question whether a non-uniform distribution of taxa exists can in general only be asked at the spatial scale of thousands of kilometers. The observed distribution patterns can thus only be discussed relative to the highest biogeographical divisions as are holarctic, neotropic, paleotropic... regions. Only for a few species, sufficient and critically evaluated data exist to give a more precise picture of their actual distribution.

(Sub-)cosmopolitan taxa

Morphologically well defined species with a wide sub-cosmopolitan distribution certainly exist in freshwater habitats. This is the case, for example, for *Mastigocladus laminosus* (Cohn ex Born. & Flah.) Kirchn., a branching blue-green alga occurring in thermal springs in a temperature range of 45–60 °C. This species thus lives within a narrow range of ecological factors, yet it is found in corresponding localities almost all over the world. Similar wide geographical distributions exist

for other blue-green algal species from less extreme environments (e.g. *Chroococcus turgidus* (Kütz.) Näg., *Microcystis aeruginosa* (Kütz.) Kütz., *M. wesenbergii* (Kom.) Kom., *Oscillatoria agardhii* Gem., *Oscillatoria splendida* Gom., *Phormidium autumnale* C. Ag. ex Gem., *Lyngbya major* Gem., *Nostoc commune* Vauch. ex Born. & Flah.). As is demonstrated in the case of *Mastigocladus* this does not mean that these species are ubiquitous occurring as well on soil, in alkaline lakes, in brackish waters, for even these species have specific ecological demands. Their wide distribution is thus mosaic-like, reflecting the corresponding distribution of habitats. It could be demonstrated at least in one case, that taxa with a large distribution are also genotypically related. Thus DNA/DNA hybridization results between strains of *Trichormus variabilis* (Kütz. ex Born. & Flah.) Kom. & Anagn. [= *Anabaena variabilis* Kütz. ex Born. & Flah.] originating respectively from the United States and Europe show that they belong to the same species when bacteriological species criteria are applied (Stulp & Stam, 1984). It is clear, however, that a certain microheterogeneity exists within cosmopolitan freshwater taxa. This heterogeneity can sometimes even be shown at the level of the same population. Besides morphology (e.g. Golubic 1965; Fjerdingsstad, 1969; Komárek, 1985), this could for example be shown for contents of pigments (e.g. Aakerman et al., 1992; Meffert & Krambeck, 1977), the ability of chromatic adaptation (e.g. Kohl & Nicklisch, 1981), toxin production (e.g. Kangatharalingam & Priscu, 1993; Llukainen et al., 1993), odorous compounds production (e.g. Skulberg & Skulberg, 1985) or isozyme patterns (e.g. Kato et al., 1991; Komárek 1994; Stulp & Stam, 1984).

Pantropic/holarctic taxa

The analysis of the currently available floristic data reveals that planktonic freshwater species with a more restricted distribution exist (Komárek, 1975, 1985; Meffert, 1989). Many of these are distributed in more or less large latitudinal bands around the world and have a pantropic or a (temperate) holarctic distribution. This is certainly the case for some tropical species (e.g. *Aphanizomenon volzii* (Lemm.) Kom., *Arthronema africanum* (Schwabe & Simons.) Kom. & Lukavský, *Cylindrospermopsis raciborskii* (Wolosz.) Seenayya & Subba Raju, *C. philippinensis* (Tayl.) Kom., *Gloeotrichia pilgeri* Schmidle (Figure 1), *Spirulina gigantea* Schmidle, *Anabaena fuellbornii* Schmidle, *A. iyengarii* Bharadw., *A. leonardii*

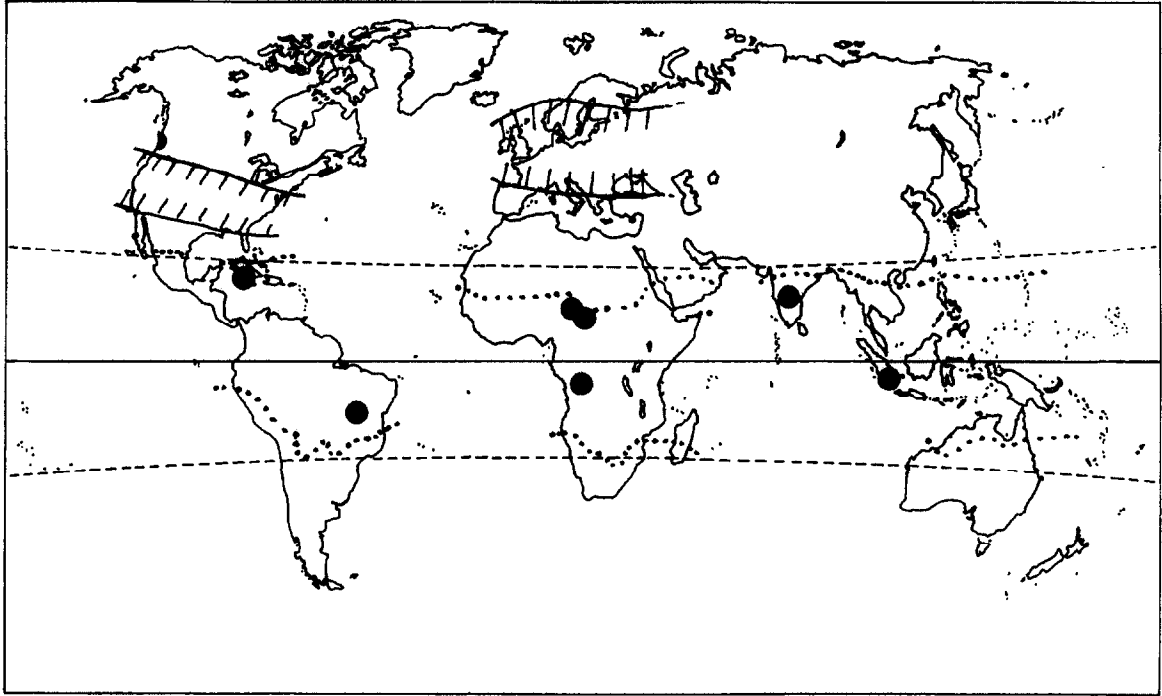


Figure 1. Examples of the distribution of pantropical/holarctic blue-green algal species. *Aphanizomenon flos-aquae* (after Komárek, 1975); ● *Gloeotrichia pilgeri* (after Komárek, 1985); ··· 20 °C winter isotherms in both hemispheres.

Comp., *A. oblonga* De Wildem., *A. recta* Geitl., *Anabaenopsis tanganyikae* (G.S. West) Wolosz. & Mill.) never found in algologically well studied temperate areas. *Oscillatoria limosa* Gem., *O. rubescens* Gem., *O. redekei* Van Goer, *Anabaena solitaria* Klebahn, *A. flos-aquae* Born. & Flah., *A. lemmermannii* Richt., *A. macrospora* Klebahn, *A. planctonica* Brunnth., *Anabaenopsis arnoldii* Aptekarj, *A. milleri* Voronikhin, *Aphanizomenon flos-aquae* Ralfs ex Born. & Flah. (Figure 1), *A. issatschenkoi* Proschk.-Lavr. are examples of planktonic blue-green algal species probably restricted to the temperate zones. A discrete area restricted to the temperate zone could also be established for the benthic freshwater species *Nostoc pruniforme* C. Ag. ex Born. & Flah. (Mollenhauer, 1970).

This distribution pattern is also observed for a number of aerophytic (*Porphyrosiphon notarisii* (Menegh.) Kütz. ex Gem., *Scytonema millei* Born. & Thur. ex Born. & Flah., *S. guyanense* (Mont.) ex Born. & Flah., Hoffmann unpublished) and marine blue-green algae (Hoffmann, 1993, 1994).

Endemic taxa

Besides these widely distributed blue-green algae, species with a regional distribution exist. Even species endemic to a small area cannot be ruled out. Thus for example *Nostoc* known from the W. Baltic region (Mollenhauer, 1970; Komárek, 1985), *Pulvinularia suecica* Borzi is only recorded from Swedish lakes (Rott & Hernandez-Mariné, 1994). In tropical regions the existence of endemic species is less well established, especially due to the lack of floristic surveys in many regions. Thus many taxa instead of being endemics of a particular region probably have a pantropical (to warm temperate) distribution. Thus *Mastigocladopsis jogensis* Iyengar & Desik. (Figure 2) described in the forties in India (Iyengar & Desikachary, 1946) was not found again until a few years ago in Corsica (Hoffmann, 1990a). The same is true for other genera (e.g. *Doliocatella* (Figure 2), *Stauromatonea*) for a long time only known from the type locality. Other species, like *Aphanizomenon manguinii* Bourr. (Figure 2) and *Trichormus subtropicus* (Gardn.) Kom & Anagn. [= *Anabaena subtropica* Gardn.], recorded on several islands in the Caribbean region (Komárek,

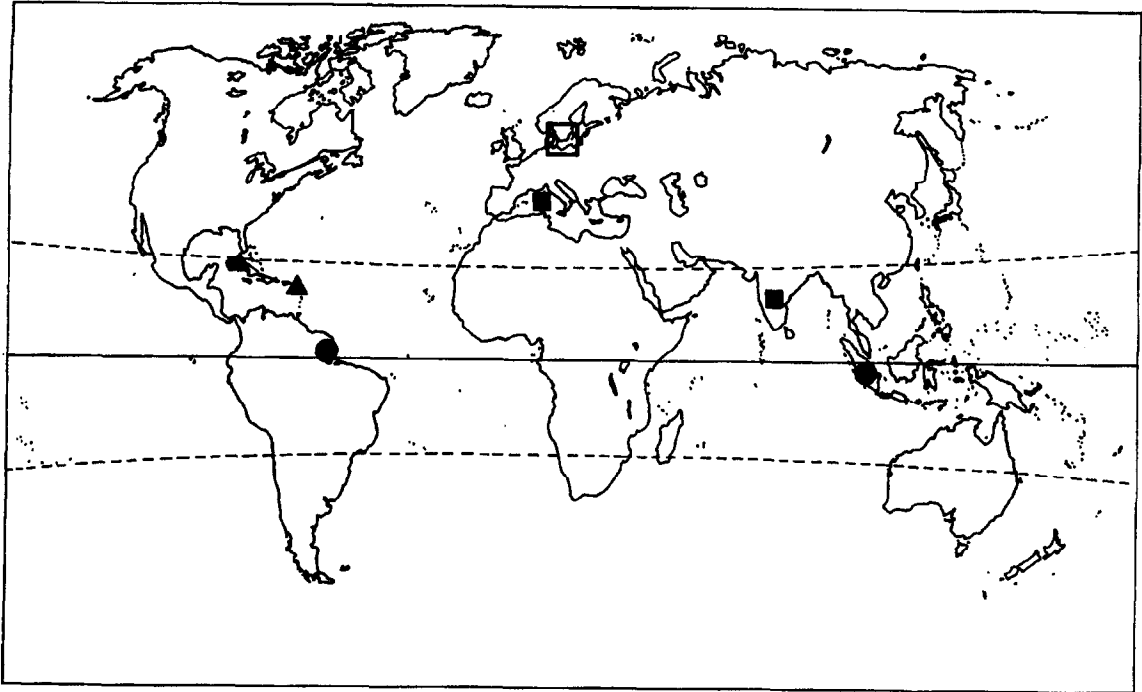


Figure 2. Examples of the distribution of endemic and pantropical, rare blue-green algal species. ▲ *Aphanizomenan manguinii*; ● *Doliocattella formosa*; ■ *Mastigocladopsis jogensis*; □ *Nostoc zetterstedtii*.

1985), may prove in the future to be true endemics. Similar restricted distribution areas also seem to exist for marine (Hoffmann, 1994) and terrestrial (Hoffmann, 1990b) blue-green algae.

In conclusion, the analysis of the currently available data of morphologically unambiguously defined freshwater blue-green algae indicates that beside cosmopolitan taxa, taxa with a more restricted holarctic or pantropical distribution exist. Even the presence of endemic species cannot be ruled out.

Possible explanations of distributions

Due to the absence of precise distribution limits for almost all blue-green algal species, it is difficult to formulate hypotheses about the factors which control their distribution. Several possible explanations addressed below are related to the ecophysiology and dispersal capacities of the different species.

Temperature

At the present level of precision, differences in the distribution of blue-green algae can almost only be considered in relation to the topographic features of the earth such as the position of the continents, or to latitude which overall determine the for algae important environmental factors that are light and temperature.

It is tempting to suggest that temperature is one of the controlling factors restricting certain species to a particular latitudinal zone. When the summer and winter isotherms are compared with the distributional boundaries of freshwater blue-green algae, a good agreement is observed for a number of species between the northern and southern boundaries of pantropical species and the 20 °C winter isotherm in both hemispheres (Figure 1). The same situation is observed for marine (Hoffmann, 1994) and terrestrial (Hoffmann, unpublished) species. Beside the absolute minimum and maximum temperatures, the annual fluctuations may also be of importance: these are smallest in polar and equatorial waters, greatest in the temperate zone. Species of the latter zone are thus expected to be the

most tolerant of temperature variations, whereas strictly tropical or polar species should be stenothermal.

Experimental evidence for the inferred hypothetical limiting effect of temperature on survival and growth of freshwater blue-green algal species is, however, scanty (except for hot spring species) and partly contradictory. Results from studies of the effect of temperature on the growth of planktonic blue-green algae from temperate zones showed that these species (*Aphanizomenon flos-aquae*, *Oscillatoria redekei*) were unable to grow at 35 °C with *Anabaena flos-aquae* even showing poor growth at 25 °C (Foy et al., 1976), but this was also true for the cosmopolitan species *Oscillatoria agardhii*. In their study on freshwater *Anabaena* s.l. species, Stulp et al. (1984) showed that the strains attributed to the cosmopolitan species *A. cylindrica* Lemm. and *Trichormus variabilis* had a sharp high temperature boundary near 32 °C and a low temperature limit of 17 °C. All the strains originated from temperate regions (England, The Netherlands, The United States). On the other hand, a strain of the widespread *A. sphaerica* Born. & Flah. isolated from India did not grow below 25 °C, but grew up to 35 °C; a similar response (however with a high temperature limit of 40 °C) was observed for the tropical species *Trichormus randhawa* (Venkat.) Kom & Anagn. [= *A. randhawa* Venkat.]. The high temperature range for growth of these strains thus agrees with the temperature of the original habitats, but not necessarily with their global distribution pattern. On the contrary, in an investigation of ten *Phormidium autumnale* strains from different parts of the world (Komárek, 1972), a certain variability in the response of the strains was observed and the temperature requirements of individual strains did not depend on the temperature conditions of the original locality.

Distribution of habitats

We already mentioned the relation between the distribution of the freshwater blue-green algal species and the distribution of ecological niches. This relationship is especially demonstrated for extreme habitats, like hot springs. Thus the cosmopolitan distribution of *Mastigocladus laminosus* can be explained by the worldwide occurrence of thermal springs. But, this idea of limited ecological types is almost always supported by detailed morphological investigations (Komárek, 1994), also for species from less extreme habitats. The tropics are known for their high diversity of habitats, many of which are not present in temper-

ate regions, e.g. rainforests, lateritic soils. It is possible that this has led to the evolution of morphological types adapted to these special biotopes (Komárek, 1985) which could explain the latitudinal distribution patterns of many species.

Dispersal

Although it is well established that different biotopes are inhabited by a specific blue-green algal flora, the opposite statement is not necessarily true, i.e. the distribution of blue-green algal species does not have to be the mirror of the distribution of corresponding niches or environmental conditions. Indeed, the absence of species on whole continents can generally not be explained on the basis of unsuitable habitats. Thus, the microbial dogma that everything is everywhere and that the environment only selects seems not to be verified for all blue-green algal species; other factors may be involved. One of these factors is dispersal.

Dispersal capacities. Whereas many aerophytic blue-green algal species are able to tolerate desiccation for long periods (e.g. Lipman, 1941) and are resistant to low as well as to high temperatures (Booth, 1946; Cameron & Blank, 1966), this is not the case for many aquatic species which live in an environment where temperature variations are generally small. It was shown for several freshwater species that desiccation and subsequent rewetting of the trichomes leads to a rapid lysis of the cells (e.g. Geitler, 1982; Stroh, 1938). The aquatic species, except for those which produce resting stages (akinetes), seem thus to be less adapted to long distance dispersal by air. On the basis of the dispersal capacities (tolerance of desiccation), it is possible to explain the extent of the distribution areas of the different *Nostoc* species (Mollenhauer, 1986).

Earth history and dispersal. Since the Precambrian, the earth surface has been in constant change. There were for example volcanic eruptions and glaciations creating new habitats and modifying the environmental conditions. If these creations of new habitats are recent enough or/and if the dispersal rate of freshwater blue-green algae is low, this could explain the absence of species in certain regions. An example of this phenomenon may be found within thermal water species.

In some regions, such as Iceland and the Azores, the blue-green algal flora found in thermal springs is species poor compared to hot springs of similar temperature and chemistry in other parts of the world (Casten-

holz, 1969, 1978). Thus, narrow-celled *Synechococcus* species are entirely missing in both areas.

Iceland was for a long time covered by an almost complete glacial cap and the thermal waters of this island have been exposed to colonization for no longer than 8000 to 10000 years. The Azores are of volcanic formations and the probable origin of hot springs dates from the late Tertiary ($20 \cdot 10^6$ year). The nearest hot springs are often several thousands of kilometers away. However, the inoculation with obligate thermophilic species generally requires, however, direct transport from another hot spring. Whereas numerous agents are available for short distance transports via insects (Brock et al., 1969), this is, except for transport by wind and birds, not true in the case of long distance dispersal. Airborne transport of certain of these species, like *Mastigocladus laminosus*, a species surviving room dryness at 25 °C for several months (Castenholz, 1970) and freezing for one year (Castenholz, 1983), over long distances seems possible; thus *M. laminosus* was already isolated after about 7 years following the formation of the volcanic island of Surtsey, probably brought in from hot springs located on Iceland at a distance of about 80 km (Castenholz, 1983). For other species (*Synechococcus* spp., *Oscillatoria* spp.) this type of dispersal seems unlikely due to their degree of sensitivity to the environment outside of their actual habitat and to the improbability of viable inoculum being located anywhere else than in hot springs (Castenholz, 1983). The time available for the colonization of the hot springs on Iceland and on the Azores by the latter species may thus have been short enough to account for the poorer flora. Thus time seems a possible factor to explain the distribution of thermophilic blue-green algae and dispersal a major barrier for at least some thermophilic blue-green algae (Castenholz, 1978).

Speciation and dispersal. The establishment of a cosmopolitan, pantropic or holarctic flora depends on an efficient distribution in relation to the rate of evolution. The evolution of blue-green algae, asexually reproducing prokaryotes, depends on the rate of new genotype formation subject to natural selection. Thus if the dispersal rate of new genotypes is greater than the rate of evolution, a pantropic or holarctic flora will result. On the opposite, if the rate of dispersal of new genotypes precedes more slowly than the rate of evolution, floristic regionality will result and would explain regional or endemic species. The evolution of new taxa may thus have occurred during a time span insufficient to

provide much likelihood yet of successful long distance colonization. The question when speciation took place in the blue-green algae and whether speciation is still going on today is unsettled (Castenholz, 1992). Blue-green algae are a very old group and already 3.5 milliard years ago forms occur which are morphologically similar to what we know now (Knell & Golubic, 1992). The general shapes of blue-green algal phylogenetic trees inferred from rRNA sequences (e.g. Giovannoni et al., 1988) indicate an early radiation of the group and a long separate evolution within each branch. The DNA homology studies within the genus *Anabaena* (Stulp & Stam, 1984) show a high degree of genetic relationship between the species which contradicts their apparently high evolutionary age.

The distribution of the 'thermal red' *Oscillatoria terebriformis* Gem. and of high temperature strains of *Synechococcus lividus* Copel. may reflect the limited spread of two relatively new taxa which may have evolved in specific springs in the Western part of the United States. Four temperature strains are distinguished within *Synechococcus lividus*. The high temperature strain is characterized by successful growth at 70 °C and is only known from North America, whereas the other strains are also known from Guatemala, Japan, New Zealand, Central Africa. The red form of *Oscillatoria terebriformis* is also only known from Western United States (Oregon, North California, Nevada, South Idaho, Montana) and could not be localized in other parts of the world (Castenholz, 1983). The dispersal of these taxa is difficult because of their inability to survive desiccation or low temperatures near zero. If we admit that the dispersal of these organisms is similar to that of other thermal water species, a relatively recent origin of these taxa is probable. The alternative is that they represent relicts from a previously more global distribution (Castenholz, 1983).

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