Cyanobacterial Responses to UV Radiation

19

Richard W. Castenholz and Ferran Garcia-Pichel

Contents

R.W. Castenholz (✉)
Institute of Ecology and Evolutionary Biology, University of Oregon, Eugene, OR 97403-5289, USA
e-mail: rcasten@uoregon.edu

F. Garcia-Pichel
School of Life Sciences, Arizona State University, Main Campus, Tempe, AZ 85287-45, USA
e-mail: ferran@asu.edu

Summary

The influence of ultraviolet radiation (UVR) on populations of microorganisms has been the subject of serious investigation for at least the past 20–25 years. UVR that is applicable to the Earth's surface (past or present) is arbitrarily divided into UVA (400–320 or 315 nm), UVB (280–320 or 315 nm), UVC (~180–280 nm). Although essentially all organisms are affected by UVR, microorganisms show more rapid, immediate and measurable effects than macro-organisms. This chapter is mainly relegated to UVR and cyanobacteria, although UV effects on other phototrophs and microorganisms, when relevant, will be included. Some ancestors of living cyanobacteria, the oldest oxygenic organisms, may have evolved in the Archean or early Proterozoic Eons, from 3.5 to 2.5 Gyr, respectively, in a time when UV radiation fluxes reaching the surface, particularly UVB and UVC, were much higher than at present. The latter wavelength region (UVC) does not reach the Earth's surface at present. Thus, cyanobacteria and other microorganisms in that distant age had to have evolved a strategy to tolerate these greater levels of UV radiation, and at present this strategy may demonstrably involve multiple devices, even within one organism. The best understood in the past several years for numerous organisms has been the active metabolic strategies that compensate for the destruction of vital genetic components, such as the development of efficient metabolic DNA repair systems. The implementation of gliding motility system for escaping the effects of high visible and UV radiation has been better described and understood. Some of the most revealing results in the last 10 years have been an almost complete understanding of the regulation of the UV-protective compounds, scytonemin and mycosporine-like compounds, that partially or completely avoid the damage caused by UV radiation.

B.A. Whitton (ed.), *Ecology of Cyanobacteria II: Their Diversity in Space and Time*,
DOI 10.1007/978-94-007-3855-3_19,

19.1 Introduction

Because of the potential to negatively affect molecules and processes of biological importance, ultraviolet radiation (UVR) is considered a detriment to all life forms. There are a few exceptions where UVR may mediate some beneficial responses to high light intensity such as the UVA role in photoreactivation of damaged DNA, and, in some cases, the regulation of some biosynthetic pathways. Although UVR represents only a small proportion of the solar radiation reaching the earth's surface, its effects are inordinately great. There have been several reviews in recent years on the effects of UV radiation (UVR) on microorganisms (e.g. Castenholz and Garcia-Pichel 2000; Vincent and Neale 2000; Whitehead et al. 2000; Roy 2000; Häder 2001; Cockell 2001; Day and Neale 2002; Shick and Dunlap 2002; Hockberger 2002; Castenholz 2004; Singh et al. 2010). This review follows the general pattern of the presentation of Castenholz (2004) and will be focused almost entirely on cyanobacteria. However, when relevant, UVR effects on other organisms will be included. In the natural habitats of cyanobacteria, UVR has a negative effect, particularly during the period of highest solar radiation. If these cyanobacteria are active metabolically, they have the ability to partially ameliorate these negative effects of UVR radiation by various repair mechanisms, often during periods of low light or darkness. Some cyanobacteria that produce the extracellular UV-absorbing compound, scytonemin, may be protected from UVR damage during periods of metabolic inactivity, such as during desiccation or dormancy as a result of suboptimal temperature or freezing (Castenholz and Garcia-Pichel 2000; Castenholz 2004).

Current paleobiological evidence suggests that oxygenic photosynthesis evolved during the early Proterozoic (~2.45–2.32 Gyr, or possibly earlier; Knoll 2008). When the ancestors of cyanobacteria first appeared, the impact of UVR radiation was undoubtedly greater than at present, due to the near lack of O_2 and ozone in the atmosphere, although the luminosity of the sun was diminished during this period. Throughout the Proterozoic, particularly by 2.0 Gyr, cyanobacterial "look-a-like" micro-fossils dominated the presumed photosynthetic picture until about 0.54 Gyr, the end of the Proterozoic (Knoll 2008). Although a high temperature environment has been proposed for the period of early life during the Archean, recent evidence suggests that the Paleoarchean ocean temperatures were no higher than about 40°C (Hren et al. 2009). In this geologic period, before the advent of efficient grazing animals, shallow seas bounding the continental or island land masses were inhabited by cyanobacterial ancestors that formed a variety of microbialites, laminated or not. It is not known when cyanobacteria first invaded terrestrial habitats. However, evidence of microbes in anoxic sediments have been documented as early as 2.75 Gyr instead of the previous suggestion of 1.2 Gyr (Rasmussen et al. 2009). Today there is a much greater variety of both aquatic and terrestrial habitats than in the early Proterozoic or late Archean, and these usually harbour cyanobacteria. Some are exposed to high UVR. UVC (~180–280 nm) was probably quite relevant during these early geologic periods, since it is absorbed by O_2/O_3 in the stratosphere, and only 10^{-5} PAL O_2 (present atmospheric level) was present according to Kasting (1987) and Pavlov and Kasting (2002). This level would not have been sufficient to attenuate UVC or UVB. Alternative conditions that may have resulted in the attenuation of UVR in the primitive anoxic atmosphere may have been sulphur vapor composed of S_8 and other sulfur molecules (Kasting et al. 1989). Also, a high concentration of ferrous ion (Fe II) may have been present in anoxic waters to significantly attenuate UVR (Pierson 1994; Pierson et al. 1993). If no screens of this type were present, 1–4 Wm^{-2} of UVC may have reached the earth and water surface, a value similar to that of maximum intensities of UVB that presently reach the earth's surface (although 5–6 Wm^{-2} may be attained) (Kasting 1987; Cockell 2001). Garcia-Pichel (Fig. 6 in Garcia-Pichel 1998) has estimated the relative damage to a selected cyanobacterium from incoming UVC, UVB, and UVA radiation during the Archean, Proterozoic and Phanerozoic Eons. Cockell (1998) has also estimated the likely biological effects of UVR on early Earth. These estimates show that UVR must have been a very significant evolutionary force during their earliest evolutionary time. Only UVA, the deleterous effects of which are mostly due to indirect, sensitized photoxidative processes, is thought to have intensified as the partial pressure of oxygen increased in the atmosphere (Garcia-Pichel 1998).

This review will summarize the UV tolerance and avoidance strategies known in living cyanobacteria. Some of these adaptive strategies that evolved in cyanobacteria probably did so in the Archean and early Proterozoic, and may now represent relics of that time. The possible influence of UVR fluctuations on plant (and presumably algal and cyanobacterial evolution), particularly during the Cenozoic have been discussed by Willis et al. (2009). A few passive "strategies", include burial at shallow sediments, growth at greater water depths (avoidance), and the seemingly altruistic sacrifice of surface layers in microbial mats, will not be discussed here. These are forms of relegation to refugia, that imply the loss of potential habitat. Instead, biochemical aspects of tolerance, UV shielding and behavioural escape mechanisms will be discussed here. This includes recently elaborated signal responses, and biochemical pathways of mycosporine-like amino acid (MAA) and scytonemin induction and synthesis. Although it is difficult to discuss the effects and responses to the three arbitrarily defined categories of UVR (UVC, UVB, UVA), an attempt will be made to present this review in that fashion. However, at first, we will describe the habitats in which cyanobacteria are most at risk to UV exposure. The readers are referred to Castenholz and Garcia-Pichel (2000) for topics not included here.

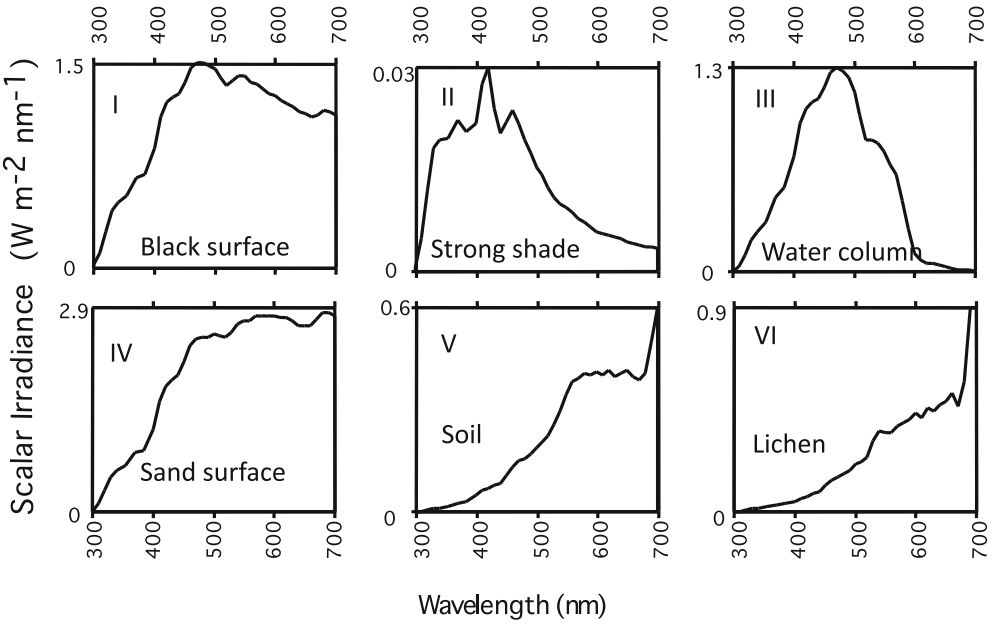

Fig. 19.1 Effects of habitat on the exposure of cyanobacteria to solar radiation: (**I**) Spectral scalar irradiance (sun and sky) incident at ground level at noon during a clear midsummer day at 41°N. Lat. (**II**) "Strong shade" habitat (N. facing surface illuminated by very diffuse sky radiation only). Although scalar irradiance is very low, the relative importance of UVR is enhanced. (**III**) Open ocean habitat (under 1 m of clear water) where all fluxes remain fairly high and UVB and visible light are more strongly attenuated than UVA. (**IV**) Surface of beach sand (quartz and feldspar) where all UVB, UVA and visible are higher than incident (by 120%, 150% and 205%, respectively) due to light trapping effects. (**V**) 300 μm deep in a wet topsoil where UVB and UVA have been attenuated below 5% of incident, but ca. 20% of visible light remains. (**VI**) Scalar irradiance within the thallus of the terrestrial cyanobacterial lichen *Collema* sp. (From Fig. 1 in Castenholz and Garcia-Pichel 2000, with references. With kind permission from Springer Science + Business Media B.V.)

19.2 UVR Exposure in Natural Habitats

Latitude determines to a great extent the flux of UVR incident at ground level, the maximum instantaneous and yearly dosage, as well as the amplitude of seasonal variation. Large seasonal variation and low maximal values are associated with higher latitudes, whereas strong, seasonal irradiances correspond to lower latitudes. High altitude, by decreasing the semi-spherical path length for atmospheric attenuation, also results in higher solar radiation fluxes. Other meteorological factors may modify the incident UVR, such as cloud cover, air pollution, and the optical thickness of the stratosphere that is regionally altered by ozone depletion (Roy et al. 1994). Industrial air pollutants, such as sulphur dioxide, nitrogen dioxide and soot particles may reduce incoming UVR by as much as 20%, thus, offsetting the potential effect of ozone depletion (Kvalevåg et al. 2009). Direct measurements of UVR are obviously preferred, but irradiance data are available from various meteorological institutions, although UVR information is often missing (Castenholz and Garcia-Pichel 2000). Total solar radiation, and the UVA and UVB components have been monitored for over 10 years in Europe and some other locations including stations in the Southern Hemisphere (see Häder et al. 2007). The measurement of UVR reaching ground level is not entirely indicative of any organism's exposure. Absorptive and scattering properties within the micro-environment of the organism may greatly modify the simple assessment of the scalar irradiance as measured by a biospherical photon collection instrument (Fig. 19.1). These modifications are not always intuitively evident or easy to measure.

Three types of "optical" habitats are first considered: planktonic, benthic, and terrestrial. Exposure in planktonic habitats is determined by the attenuation rate within the water column and by the mixing regime of the water mass. Typically, cells are subjected to high and low exposure periods as they are brought up and down by turbulence (Cullen and Neale 1994). A time integration of UV exposure per cell is very difficult to calculate in these circumstances because of complex hydrodynamic mixing processes (Castenholz and Garcia-Pichel 2000). A comparison of several natural marine waters showed that the UV doses received by cells in the euphotic zone ranged between 3% and 9% of the incident doses that would be received if they remained at the surface (Garcia-Pichel and Bebout 1996). Ultra-oligotrophic lake and most oceanic seawater are quite transparent to UVR. A detailed re-evaluation of visible and UV radiation penetration in the clearest oceanic waters was presented by Morel et al. (2007). UVA can penetrate to nearly the maximum depth of the euphotic zone (Smith and Baker 1981; Helbling et al. 1994; Prezelin et al. 1994). UVB is attenuated

more steeply, but still a low intensity may reach the limit of the euphotic depth. Turbidity, of course, will greatly reduce UVR penetration, but more selectively dissolved organic matter (DOM), particularly humic acids, a general term for coloured organic solutes that are generally derived from vegetation, especially from littoral and terrestrial sources in lakes, ponds, and river backwaters, and from near shore macroalgae in the marine environment, will have the greatest impact. (Vincent and Roy 1993; Scully et al. 1996; Karlsson et al. 2009). In many lakes, particularly during summer stratification when cyanobacterial and algal populations may be vertically stabilized in the metalimnion or upper portion of the hypolimnion, dense populations of cyanobacteria may accumulate. This is conspicuous in eutrophic and mesotrophic lakes in which dim green light zones are dominated by gas-vesiculate filamentous cyanobacteria, red in colour due to a high cell content of phycoerythrin. However, little UVR is likely to reach such depths in these waters. In terrestrial habitats, including shallow water springs and streams, ephemeral slacks, and moist surfaces, two factors locally influence the incident UVR, the orientation of the surface with respect to the solar vertical, and the albedo of the surface. Instantaneous exposure and dose are highest on surfaces oriented orthogonally to the sun's vertical, and lowest in those in the optical shadow of solids (Fig. 19.1). However, due to the atmospheric (Rayleigh) preferential scatter of the shorter wavelengths, the spectral composition of the diffuse light that penetrates the shade behind solids is highly enriched in UVR (Robinson 1966; Frederick et al. 1989). At the wavelength of 300 nm (UVB), approximately half of the incident radiation is diffuse and half comes directly from the solar disc. Thus, populations thriving on shaded surfaces will receive higher UVR doses relative to the visible than populations on sunny surfaces, but with lower absolute doses of UVR. The implication then is that UVR may play an important role for cyanobacteria exposed to diffuse light. The radiation reflected from the surface may change the absolute and spectral characteristics of the absorbed radiation with respect to the incident radiation. For example, substrates such as white sandstone and carbonaceous materials (e.g. travertine, other limestones, coral sand, and concrete) reflect UVR strongly (Koller 1965; Diffey et al. 1995). In contrast, sedimentary environments (including microbial mats) are characterized by the strong attenuation of both visible and UVR due to absorption and multiple scattering by the matrix and the organisms, so that phototrophic metabolism is restricted to thin (millimeter to centimeter) surface layers (e.g. Castenholz and Garcia-Pichel 2000; Kruschel and Castenholz 1998; Garcia-Pichel et al. 1994). When close to the surface, light-trapping phenomena result in localized irradiance radiation maxima that are higher than the incidence radiation. Typically, then, there is an onset of quasi-exponential attenuation of light below the light-trapping. Thus, in sedimentary habitats, extremely steep gradients of exposure ranging from zones of increased exposure to zones that are refuges from UVR. This condition also applies to endolithic populations in many habitats. Because light-trapping effects are greater at longer wavelengths, and absorption by particulates is most pronounced at shorter wavelengths, the ratio of UVR to visible invariably decreases with depth. A comparison of data from several sedimentary micro-environments showed that the space-averaged UVR dosage rates within the euphotic depth ranged from 15% to 33% of the incident value, a much higher UVR exposure than that in the euphotic zones of water columns (Garcia-Pichel and Bebout 1996).

A recent experiment that placed endo- and epilithic intertidal microorganisms into low orbit space at a height of about 300 km for 10 days that included exposure to vacuum, desiccation, and high intensity UVR resulted in the survival of a coccoid, aggregated cyanobacterium (Olsson-Francis et al. 2010). However, there was no information on the intensity of UVR that actually reached the endolithic cyanobacteria.

Other aspects of biologically effective UVR exposure, such as biological weighing functions are discussed in Castenholz and Garcia-Pichel (2000).

19.3 Metabolically – Timed Exposure

Cyanobacteria are often the predominant phototrophs in habitats where metabolic activity is restricted due to lack of water or nutrients, freezing or sub-optimal temperatures. Under conditions of restricted or interrupted active metabolism, the impact of exposure to solar radiation may seriously exceed that predicted by simply expressing exposure in terms of total time. Dose modification factors based on the fraction of total time that the organisms are active, can be used to obtain a more relevant metabolically-timed exposure. This may be relatively easy where the time partition is clear but quite complicated if metabolism slows rather than halts. An extreme example may be the surface-dwelling soil cyanobacteria of the Colorado Plateau (e.g. *Nostoc*, *Scytonema*, *Microcoleus*). These populations may experience about 100 h of wetness (active metabolism) during the winter season and additional scattered periods during and after summer rains (Garcia-Pichel and Belnap 1996). Approximately one half of the periods of wetness occur during daytime. However, the populations are exposed to UVR throughout the year. Thus, the UVR damage accumulated during a year's exposure needs to be rectified by repair and other metabolic processes within the possible 120 h when cells are potentially active. This represents a metabolically-timed dosage of about 70 times the actual incident dose. This metabolically-timed irradiance is likely to be a better predictive factor in the terrestrial habitat of desert crusts, in polar mats, and in alpine situations, where desiccation and/or cold are important factors. However, all of these types of theoretical calculations are nullified if the

organisms have an extracellular UVR-protectant, such as the sheath "pigment", scytonemin, or layers of dust/soil that would prevent much of the UVR from reaching the cell interior.

19.4 Examples of Cyanobacterial Habitats with High Exposure

The Proterozoic Eon (2.5–0.54 Gyr) was populated by cyanobacteria or their oxygenic ancestors, as demonstrated by micro-fossil and relic chemical evidence as well as indirectly by the early oxygenation of the waters and atmosphere (Knoll 2008). In this geologic period, before the advent of efficient grazing animals, shallow seas bounding the continental or island land masses were inhabited by cyanobacterial ancestors that resulted in the formation of a variety of stromatolites. Today there is a much greater variety of both aquatic and terrestrial habitats and niches than in the early Proterozoic or late Archean, and these usually harbour cyanobacteria. Some are exposed to high UVR.

19.4.1 Hot Springs

Although hot springs occur today in many locations associated either with volcanic activity (residual or current) or tectonic activity, most terrestrial springs are exposed to full sun because vegetation near them is usually low or absent due to high soil temperatures, and possibly toxic compounds such as arsenite and arsenate. High elevation is another factor that exposes such habitats to high levels of solar irradiance. This was pointed out by Phoenix et al. (2006) who studied hot spring cyanobacterial habitats at over 5,000 m elevation in Bolivia. However, the UVR fluxes measured (perhaps incorrectly) were no higher than those at the major thermal areas of Yellowstone National Park, most of which are close to 2,500 m. The measurements in Bolivia were also quite comparable to midday values in Argentina, some at sea level, but during a low ozone period (Orce and Helbling 1997). In Iceland, many geothermal springs occur only slightly above sea level, but no trees or shading vegetation occurs, and high levels of UVR should be expected. However, the solar angle in summer at over 65°N. reduces total solar intensity, but not necessarily 24 h dosage during the summer months. Many or most hot springs produce shallow runoffs of clear water that flows over microbial mats that are topped by cyanobacteria or simply biofilms of cyanobacteria at the upper end of their thermal range for growth (72–73°C), the highest known temperature for photosynthesis (Fig. 19.2) This limit applies to some areas in the western US and parts of southeastern Asia. However, the upper temperature limit is considerably lower (63–64°C) in other regions (including New Zealand, Iceland and Europe) (see Ward and Castenholz 2000) due to the absence of the highest temperature form of *Synechococcus* in these and other regions. Metabolic and carotenoid mechanisms for UVR damage repair occur in probably all cyanobacteria (Fig. 19.3) When hot spring runoff reaches average temperatures below about 50–55°C many cyanobacteria also produce scytonemin, an extracellular sheath UVR-shielding

Fig. 19.2 An alkaline hot spring in the Lower Geyser Basin, YNP ("Five Sisters") in summer showing upper temperature limit (70–73°C) of *Synechococcus* sp.: *yellow* cover on *left* and foreground, rich in carotenoids; *Synechococcus* sp. also in *deep shaded* basin, rich in chlorophyll and phycocyanin. *Gray* area is covered with water (>74°C), originating from spring source in *upper left*. *Dark* moist crust along *left* and *right* edge consists of various cyanobacteria containing scytonemin (Photo by RWC)

Fig. 19.3 Alkaline White Creek, Lower Geyser Basin, YNP, with a mean temperature at this point of 50–55°C, with green trailing wisps of *Mastigocladus* (=*Fischerella*), *Leptolyngbya* and *Synechococcus*, the last attached mainly to streamers of *Chloroflexus*-like anoxygenic bacteria. The *rich green* of the cyanobacteria in the fast-flowing stream is probably a result of continuous waving motion of the streamers, thus lessening constant exposure to high solar radiation. The *orange* static film of cyanobacteria fanning down the embankment is rich in carotenoids, probably because of suboptimal temperature and high solar irradiance that results in a high carotenoid to chlorophyll + phycocyanin ratio (Photo by RWC)

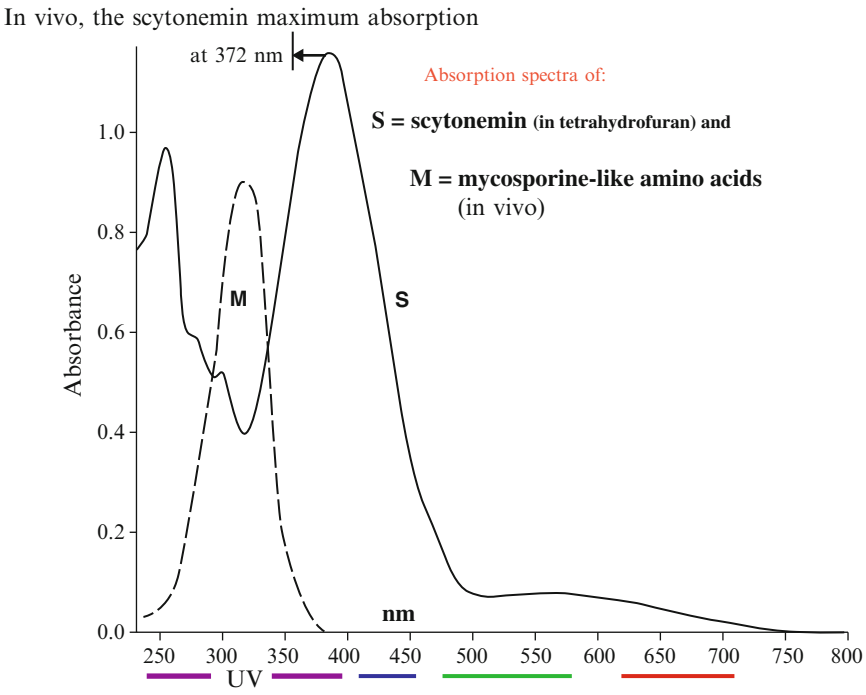

Fig. 19.4 Absorption spectrum of scytonemin in tetrahydrofuran. The *in vivo* maximum absorption peak is at 372 nm. The spectrum of a generalized MAA has been added, as well as colour guides to nm ranges (Modified from Proteau et al. 1993. With kind permission from Springer Science + Business Media B.V.)

Fig. 19.5 Alkaline Grand Prismatic Spring in Midway Geyser Basin, YNP. High temperature *Synechococcus* sp. in distance (*greenish* at edge of pool). *Orange* flow in shallow water from ~60°C to ~50°C consisting mainly of *Leptolyngbya* spp. (=*Phormidium*) and *Synechococcus* spp. The cells are rich in carotenoids and low in chlorophyll and phycocyanin content. The *brown* band (<50°C) consists mainly of *Calothrix* sp. with a high content of scytonemin in the filament sheaths (Photo by RWC)

pigment that may actually prevent damage even when the cells are metabolically inactive (Fig. 19.4). The scytonemin-producing cyanobacterial species in Yellowstone (e.g. *Calothrix, Scytonema* and *Nostoc*) are those that grow only below ~45–50°C (Fig. 19.5). It has also been shown that acidic hot springs (pH 0.5–4.0, ~35–56°C) harbour only one type of phototroph, namely the unicellular members of the Cyanidiales (Rhodophyta). In their natural shallow stream habitats they are significantly inhibited by high solar radiation, particularly UVR (Lehr et al. 2007).

19.4.2 Intertidal Marine and Hypersaline Habitats

Intertidal marine habitats close to "normal" seawater salinity (~31–35 ppt), such as mud flats and salt-water marshes are usually devoid of perennial cyanobacterial mats, probably because of an abundance of invertebrate herbivores and algal and plant competitors. Nevertheless, there are some tidal flats covered by water mainly during spring tides, and these exclude most grazing invertebrates because of desiccation and high salt intolerance as the flats dry out. Some of these flats (e.g. Laguna Guerrero Negro, Baja California Sur, Mexico) are dominated by scytonemin-producing cyanobacteria (*Lyngbya* cf. *aestuarii* and *Calothrix* sp.). These almost monospecific mats inhabit the mid-intertidal (*Lyngbya*), and uppermost intertidal (*Calothrix*) and cover vast areas in this location (Javor and Castenholz 1981, 1984). Both these cyanobacteria in nature contain scytonemin in their sheaths (Fig. 19.6). Other intertidal sedimentary habitats, such as the Great Sippewissett Marsh, Massachusetts, contain so much biogenic sulfide in the sediments that many grazers are absent or restricted, and highly exposed and cyanobacterial mats develop mainly in the summer. The benthic mats of shallow, natural or man-made, hypersaline pools and lagoons also

Fig. 19.6 Intertidal flat at Laguna Ojo de Liebre, Baja California Sur, Mexico. The *dark area* is covered by the scytonemin-rich cyanobacterium, *Lyngbya* cf. *aestuarii* during neap tide. This area is covered by seawater of 35–50‰ salinity during periods of spring tides (~every 2 weeks) (From Castenholz 2009, Mats/microbial, in encyclopedia of microbiology, Fig. 9, p 287. With kind permission of Elsevier, Inc.)

Fig. 19.7 *Stigonema* sp. from 1 m depth in ultra-oligotrophic Waldo Lake, Oregon Cascade Mountains: *Yellow* colour of sheath is caused by scytonemin. Diameter of main axis is ~7 μm (Photo by RWC)

provide habitats with high insolation where cyanobacteria usually dominate, at least at salinities above 50–60 ppt, a level that usually excludes grazing herbivores except for harpactipoid copepods, nematodes, and various "protozoa" (Des Marais 1995; Garcia-Pichel et al. 1994; Kruschel and Castenholz 1998). In warm, clear tropical waters, several types of cyanobacteria, including living stromatolite-like cushions, and both filamentous and gelatinous cyanobacterial tufts and epilithic biofilms attached to sediment, rocks, or macro-algae are exposed to high levels of UVR (Castenholz and Garcia-Pichel 2000).

19.4.3 Benthic Freshwater Habitats

Clear water lakes and streams are common in many areas distant from human populations. These include a large percentage of oligotrophic alpine/subalpine and polar lakes and ponds (Vinebrooke and Leavitt 1996; Vincent 2000). Although many of these habitats are not dominated by cyanobacteria, there are various algae that are typical. However, in ultra-oligotrophic lakes and ponds in polar regions cyanobacterial mats again become predominant, possibly because of the lesser ability of many or most eukaryotic algae to tolerate long- or short-term and frequent freezing and thawing (Vincent et al. 1993, 2004; Tang et al. 1997; Bonilla et al. 2005) and also, in some cases, because of the low herbivore diversity and density. One ultra-oligotrophic lake in the Oregon Cascades (Waldo Lake) that is essentially equivalent to distilled water in terms of solutes, is dominated by benthic populations of cyanobacterial populations of the genera, *Stigonema* and *Scytonema*, that have sheaths rich in scytonemin to depths of at least 15 m (Johnson and Castenholz 2000) (Figs. 19.4 and 19.7). These oligotrophic waters are dominated by heterocystous cyanobacteria by virtue of an extreme deficiency of combined nitrogen. Another example of this is the slow-growing giant *Nostoc* cf. *pruniforme*, forming scytonemin-containing colonies that form an almost monospecific population in a few cold water spring-fed ponds in southern Oregon that never exceed ~5°C (Dodds and Castenholz 1988; photo in Castenholz and Garcia-Pichel 2000). Although dominance by cyanobacteria in cold waters would have been unexpected some years ago, Antarctic and Arctic freshwater and saline ponds and lakes are nevertheless dominated by cyanobacterial mats (Vincent 1988; Tang et al. 1997). It was long thought that cyanobacteria were more adapted to warmer waters. It appears, however, that most of the cyanobacterial species in these habitats are simply more tolerant of cold and freezing than most eukaryotic algae, although their optimal temperature for photosynthesis and growth may be considerably higher than in their ambient cold water habitats (Nadeau and Castenholz 2000; Castenholz and Schneider 1993). Heterocystous *Nostoc* with scytonemin is very common in glacial meltwater streams and ponds in the Antarctic dry valleys (Vincent 1988; Castenholz, unpublished observations).

19.4.4 Marine and Freshwater Plankton

Although much information is available on the effects of UVR on marine, planktonic diatoms, and various photosynthetic flagellates (Gieskes and Buma 1997; Bouchard et al. 2005; Sobrino et al. 2008; Laurion and Roy 2009), there is little information on the specific effects of UVR on marine

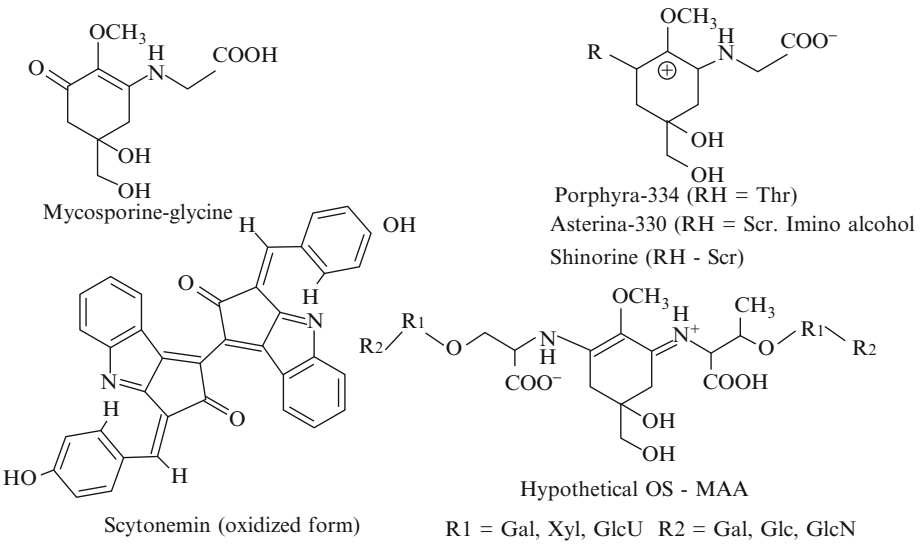

Fig. 19.8 Chemical structure of some compounds in cyanobacteria involved in UVR protection, including scytonemin and 5 types of mycosporine-like amino acids. OS-MAA is found in the EPS of *Nostoc* cf. *commune* (Ehling-Schulz et al. 1997) (From Fig. 2 in Castenholz and Garcia-Pichel 2000, with other references. With kind permission from Springer Science + Business Media B.V.)

cyano-plankton. The filamentous gas-vesiculate *Trichodesmium*, the principal N_2-fixer of warmer, nitrate-depleted oceanic waters, is subject to the production of high amounts of reactive oxygen species, including oxygen radicals due to the impact of high visible and UV radiation. It produces the highly potent antioxidant, all-trans-ß-carotene that may counter the detrimental effects of reactive oxygen (Kelman et al. 2009). *Trichodesmium* and some other marine and freshwater planktonic cyanobacteria are known to accumulate large quantities of MAAs (mycosporine-like amino acids) that are, in these cases, intracellular UVR absorbers (Fig. 19.8). However, MAAs apparently do not occur in small unicellular planktonic cyanobacteria (Garcia-Pichel and Appel, unpublished data). Meador et al. (2009) demonstrated UVR-DNA damage in surface dwelling microorganisms over a long latitudinal range (70°N–68°S in the Pacific with some consideration of the picoplanktonic cyanobacteria, *Synechococcus* and *Prochlorococcus*. UVR may penetrate to considerable depth in clear oceanic waters; in some cases UVB to over 30 m and UVA in excess of 60 m (Holm-Hansen et al. 1993; Jeffrey et al. 1996; Booth and Morrow 1997; Morel et al. 2007). However, in coastal waters UVR (and especially UVB) may show a rapid attenuation to <1% in less than 0.5 m depth (Nielsen and Ekelund 1995).

In general, high-altitude lakes are not dominated by cyanobacteria, but although cyanobacteria (*Synechococcus* sp.) predominated in several lakes of the Tibetan Plateau (~3,200–4,700 m elevation), a low taxon richness was evident (Xing et al. 2009). In any case, most subalpine and alpine lakes and ponds contain clear water and thus, have high exposures to solar irradiance. Freshwater unicellular cyanobacteria of pico-planktonic size also occur in many of these waters (Weisse 1993; Eguchi et al. 1996; Postius et al. 1996). In many temperate lakes, especially eutrophic types, gas-vacuolate cyanobacteria often predominate (e.g. *Aphanizomenon, Anabaena, Planktothrix, Limnothrix, Microcystis*) and may rise to the surface during periods of low wind and are destroyed by high solar irradiance. During such a calm period in sunlit Upper Klamath Lake, Oregon , there was there was an almost complete extermination (only phycocyanin remained) of dense *Aphanizomenon* populations that floated to the surface (Castenholz, unpublished observations).

19.4.5 Terrestrial Habitats

In exposed terrestrial habitats that are often extreme by virtue of long-term or periodic desiccation, many species of cyanobacteria thrive because of their tolerance to desiccation, but also because of a high tolerance, in many cases, to UVR (Potts 1994). The terrestrial cyanobacterial mats or crusts (often known as biological soil crusts) occur in many of the warm and cold deserts of the earth, where these may form an extensive ground cover when undisturbed by human practices, and sometimes surrounding protective desert shrubs (Garcia-Pichel and Belnap 1996; Mazor et al. 1996). The harder substrates, such as rocks and cliff faces are often covered with thin dark covers of epilithic cyanobacteria ("tintenstriche") that by virtue of their unprotected location, obviously receive much UVR whether wet or dry. Most of these cyanobacteria are dark in colour because of sheaths or EPS that contain scytonemin. These generally do not occur on the most sun-exposed faces which

are often too desiccated to allow any free-living phototrophs, except for lichens, some of which are inhabited by cyanobacterial photobionts that also contain scytonemin (Büdel et al. 1997). The well-known *Nostoc flagelliforme* of semi-desert regions appears to be insensitive to UVR under both desiccated and rehydrated conditions (Gao and Ye 2007). There is a large literature on endolithic and chasmolithic cyanobacteria within limestone (including travertine), dolomite, sandstone, and other somewhat porous rocks (Norris and Castenholz 2006). Most of these situations involve a narrow band (1–2 mm thick) 1–3 mm below the rock surface. Although only one publication has measured light penetration to the level of the phototroph band (Matthes et al. 2001), it is assumed that the specific depth of the chlorophyll band represents many strategies, such as avoidance of high light and UVR, as well as optimization of the light intensity, moisture retention, and prevention of erosion by wind. Such endolithic populations are known world-wide in hot and cold, deserts (e.g. Nienow and Friedmann 1993) as well as in rocks exposed to seasonal desiccation, wetting, and freezing, such as in travertine in Yellowstone National Park and the Rocky Mountains (Norris and Castenholz 2006; Walker and Pace 2007). Some isolates of the desiccation tolerant *Chroococcidiopsis* (a unicellular cyanobacterium) are also capable of tolerating up to 5 kGy of ionizing radiation (X-rays), while desiccated, and may be comparable to the tolerance and DNA repair mechanisms of *Deinococcus,* a heterotrophic bacterium well-known for this ability (Billi et al. 2000).

19.5 Negative Effects of UVR and Physiological and Biochemical Strategies of Counterbalance

The targets of damage by UVR with respect to metabolism, DNA, development, and behaviour for cyanobacteria were summarized in Table 1 in Castenholz and Garcia-Pichel (2000), while studies on the effects of UVR on the morphology of filamentous cyanobacteria have been reported by Wu et al. (2005) and Gao et al. (2008). Summaries of the effects of UVR on other organisms were summarized by Jägger (1985), Häder (2001), and Hockberger (2002). The number of targets and detrimental effects mount exponentially with shortening wavelengths (Jägger 1985; Whitehead et al. 2000). However, under standard conditions of environmental exposure, UVC is no longer environmentally relevant, because of complete atmospheric absorption. Since UVC and UVB radiation have the most lethal effects, and because these spectral regions reached the Earth's surface without atmospheric interference only in the Archean and early Proterozoic, they will be discussed first.

19.5.1 UVC and UVB

Germicidal lamps that emit in the UVC range have been used in many experiments with bacteria, viruses, DNA and proteins (see Jägger 1985). Damage is mainly through direct absorption by DNA. DNA absorbs in three spectral regions: I (with a peak at 260–264 nm), II (with a peak at 192 nm), and III (below 125 nm). Spectral regions II and III would only have relevance in outer space (see Zalar et al. 2007a, b; Olsson-Francis et al. 2010). The effect of UVC radiation (254 nm max) negatively affected short-term photosynthetic rate and survival in *Agmenellum quadruplicatum* (now *Synechococcus* sp. PCC 73109)(Van Baalen 1968). However, the damage to DNA was cured by photoreactivation at wavelengths from ~395 to 450 nm (Van Baalen and O'Donnell 1972).

Chloroflexus aurantiacus, a primarily photoheterotrophic anoxygenic bacterium, showed relatively high UVC-tolerance which may have had relevance during the Archean when the Chloroflexi may have evolved (Pierson et al. 1993). Results of continuous UVC radiation within the possible Archean limits, resulted in yields similar to those of controls under anoxic conditions at 0.01 Wm^{-2} UVC, an intensity that severely inhibited *E. coli.* This exposure could not occur indefinitely without DNA damage and deleterious accumulation of mutations. Pierson et al. (1993) suggested that the Archean sediments may have carried a load of ferric and ferrous ions that blocked UV wavelengths, but still passed the longer visible wavelengths that support photosynthesis.

Cyanobacteria that inhabit exposed, near-surface habitats usually synthesize the UVR-absorbing pigment, scytonemin, in their sheaths or EPS. This compound has major absorption maxima in the UVC and UVA spectral regions, but also ample absorption in the UVB (Proteau et al. 1993) (Fig. 19.4). During the early Precambrian an extracellular compound that absorbed UVC may have been of considerable benefit. O_2 is a requirement for scytonemin synthesis, but internal O_2 release as a product of oxygenic photosynthesis must have occurred long before the general oxygenation of the waters. Although scytonemin functions primarily today as a UVA and UVB screen, Dillon and Castenholz (1999) found that it afforded considerable protection against UVC photosynthetic damage in scytonemin-containing *Calothrix* and *Chroococcidiopsis* cultures when 0.5–1.0 Wm^{-2} UVC radiation was added to natural solar irradiance. Many intracellular and extracellular compounds absorb in the UVC region, however, the presence of scytonemin in the external sheath provided protection that the glycan sheath without scytonemin did not.

UVB is less potent energetically than UVC, but the type of damage is similar. UVB includes the wavelengths that are most harmful to humans by causing sunburn and skin cancer (e.g. melanoma). The recent increase in UVB in some regions

is due to periodic stratospheric losses of ozone. The UVB (280–315/320 nm) intensity reaching the earth's surface is sufficient to cause damage to many cellular components in micro-and macro-organisms, including DNA as a direct target. The result is the formation of various photoproducts (e.g., cyclobutane-pyrimidine dimers, pyrimidine (6–4) pyrimidone products, and cytosine products) (Ravanat et al. 2001). Purine bases are also photoreactive. Other impairments include accelerated degradation of photosystem II proteins (e.g. D1/D2) and destruction of the light-harvesting phycobiliproteins, since these have a small absorbance peak in the UVB (Lao and Glazer 1996; Wingard et al. 1997). Also, various activities such as synthesis of chlorophyll, energy transfer in light harvesting, nitrogen fixation, RUBISCO and ATP synthase activities, nitrate and ammonium uptake, nitrogen fixation, motility and photoorientation, and cell differentiation are negatively affected by UVB radiation (Häder 1984; Sass et al. 1997; Choi et al. 1999; Castenholz and Garcia-Pichel 2000). UVB damage may be more severe under nutrient limitation. Damage to light-harvesting complexes in cyanobacteria may exceed the damage to DNA in some cases (Lao and Glazer 1996). D1/D2 proteins of PS II reaction center may be destroyed not only directly by UVR but also indirectly by reactive oxygen produced by high intensity violet/blue light or UV radiation. Rapid *de novo* synthesis of D1/D2 proteins is an essential part of the repair process (Sass et al. 1997). Several proteins may be photooxidized by UVB radiation since tryptophan, tyrosine, phenylalanine and histidine absorb in the 290–315 nm range (MacDonald et al. 2003). In one case, photooxidative inhibition and damage by moderate UVB was reversed after about 2 weeks of continuous exposure in a species of *Anabaena* (He et al. 2002). MacDonald et al. (2003) found that a naturally high ratio of visible light to UVB resulted in a greater tolerance to UVB in *Synechococcus* PCC 7942.

The exposure of the same unicellular cyanobacterium (*Anacystis nidulans* R-2 = *Synechococcus* PC 7942) to UVB and UVA resulted in the production of several "UV-shock" proteins, some of which may function as enzymes that scavenge reactive oxygen molecules (Shibata et al. 1991). Earlier, the induction of the synthesis of a few specific proteins in thermophilic *Phormidium* cf. *laminosum* was reported in response to inhibitory UV radiation (Nicholson et al. 1987). Another study, again using *Synechococcus* PCC 7942, has demonstrated that an ATP-dependent Clp protease is essential for acclimation to UVB, and results in the rise of a modified D1 PS II protein (D1:2) that is more resistant to UVB stress (Porankiewicz et al. 1998). The *psbA* genes (*psbA2* and *psbA3*) that code for a more UVB tolerant, PS II D1 protein may be activated in *Synechocystis* PCC 6803 under even low levels of UVB exposure (Máté et al. 1998; Campbell et al. 1998). After 2 h exposure of *Synechocystis* PCC 6803 to 20 μE m^{-2} s^{-1} UVB the levels of expression of 55 genes rose more than twofold and those of 44 genes fell more than twofold (Los et al. 2008). With whole genome profiling of some phototrophic prokaryotes now possible, transcripts from genes involved in various light (or UVR) intensity transitions can be probed with full genome DNA microarrays (see Gill et al. 2002; Los et al. 2008).

UVB affects shallow benthic phototrophs, (e.g. in intertidal flats, shallow lagoons and lakes), also phytoplankton, especially in clear oceanic waters where harmful intensities may reach over 20 m (much less in turbid or waters rich in coloured dissolved organic matter), as well as exposed terrestrial crusts and epi- and endo-lithic populations of cyanobacteria and microalgae. There is a particularly large literature on the effects of UVR (mainly UVB) on phytoplankton which often includes diatoms, dinoflagellates, and other micro-algae, but there is little specific information on the well described cyanobacterial picoplankton, such as *Synechococcus*, *Prochlorococcus* and the less well-known *Crocosphaera.* Effects of UVB in lakes and the sea are particularly difficult to assess because of vertical and horizontal mixing and, thus, like other field studies, requires extrapolation of short term daylight results to full days, weeks and seasons (Day and Neale 2002). Nevertheless, work in the Southern Ocean by various investigators have estimated that phytoplankton productivity has been reduced by ~0.2–2.4% as a result of increased UVB that was presumably due to periodic ozone depletion. However, estimates of this type differ greatly (see Day and Neale 2002 for references). As with UVC, some of the negative effects on DNA (formation of cyclobutane pyrimidine dimers and 6–4 photoproducts that block DNA and RNA polymerases) may be repaired by photoreactivation, utilizing UVA and/or violet/blue wavelengths that are absorbed by chromophores of photolyase, a DNA-bound enzyme that restores the intact bases, and also by nucleotide excision repair (Jägger 1985; Sancar 1994, 1996). Increases in temperature have been shown to enhance the DNA photoreactivation repair rates in algae (Pakker et al. 2000).

In an extensive review, Bailey and Grossman (2008) have discussed the evidence that a photoprotective method of dissipating excess photon (quantum) energy by the light-harvesting complex is by down-regulating the transfer of this excitation to the photosynthetic reaction centres. This is termed non-photochemical quenching (NPQ), and the authors have concluded that this process also occurs in cyanobacteria although only previously known in algae and plants. NPQ in cyanobacteria appears to involve the absorption of blue light by a carotenoid-binding protein and probably involves quenching in the phycobilisome core. Although these reactions are known only for the short wavelength visible spectrum, it is possible that excess UVR absorption may be dissipated by a NPQ quenching reaction as well.

Sytonemin has substantial absorbance in the UVB spectral region. However, the degree of protection afforded specifically by scytonemin has not been tested in this spectral region (Fig. 19.4). It may, however, be insufficient, as most scytonemin synthesizers complement their sunscreen capabilities with mycosporine-like amino acids (MAAs), Mycosporine-like amino acid derivatives (MAAs) are known in very many cyanobacteria (Garcia-Pichel and Castenholz 1993), numerous microalgae, and marine zooplankton (Castenholz and Garcia-Pichel 2000; Shick and Dunlap 2002). MAAs are low molecular weight, water soluble compounds that are condensation derivatives of a cyclohexenone ring and amino acid (or imino alcohol residues), but are acquired secondarily by invertebrates through consumption of primary producers (Fig. 19.8) Radiotracer experiments have shown that in cyanobacteria the core cyclohexenone is derived from the shikimate pathway, and amino acids are condensed onto it directly as precursors (Portwich and Garcia-Pichel 2003). Gadusols, that are putative intermediates in the shikimate pathway of MAA synthesis, may have been early absorbers of UVC/B radiation and may also have served as strong antioxidants (Shick and Dunlap 2002). The absorption peaks of MAAs range from 310 to 360 nm (i.e. from UVB into the UVA) (Fig. 19.4). Short wavelength MAAs are monosubstituted and direct precursors of more derived, bi-substituted, long wavelength MAAs (Portwich and Garcia-Pichel 2003) In most cyanobacteria, they are synthesized when exposed to UVB. However, in all but one of the cyanobacteria examined (*Nostoc*), these compounds occur in the cytoplasm and could serve as alternative targets for perhaps only about 10–30% of UVB photons penetrating a cell (Garcia-Pichel and Castenholz 1993, Garcia-Pichel et al. 1993). In cells of small diameter (<10 μm), the beneficial effect would be negligible (Garcia-Pichel 1994). MAAs appear to be important in some way in UVB protection, since they are so tightly associated with UVB exposure. Perhaps, MAAs have an unknown function that is merely associated with UVB exposure (Shick and Dunlap 2002). It is apparent that intracellular MAAs cannot provide complete protection from UVB/A radiation. Some species of cyanobacteria apparently do not synthesize MAAs or scytonemin, and therefore utilize only metabolic repair mechanisms for UVB damage (Quesada and Vincent 1997). However, the employment of migratory escape motility in some may avoid UVR exposure altogether (see behavioral strategies later). In terrestrial *Nostoc* cf. *commune*, however, MAAs are bound to oligosaccharides in the inner external glycan sheath (EPS), with scytonemin in the outer portion (Ehling-Schulz et al. 1997; Ehling-Schulz and Scherer 1999). In this case, then, there is no doubt that MAAs, together with scytonemin, provide a nearly perfect spectral shield against UVB as well as UVA (Fig. 19.8). The UV energy absorbed must be dissipated, which is no problem within the sheath, but intracellular absorption may result in transfer of energy to sensitive molecules. Many cyanobacteria synthesize one or more MAAs even if they have no extracellular sheath or EPS. However, it is probable that most or all sheathed scytonemin producers are capable of making MAAs either constitutively or by UVB induction (Garcia-Pichel and Castenholz 1993). Various MAAs are induced through the absorption of UVB radiation (Ehling-Schulz et al. 1997; Sinha et al. 2001). However, Portwich and Garcia-Pichel (1999) have shown that either UVB or osmotic stress induced MAA synthesis in a strain of *Chlorogloeopsis*. The photoreceptor involved in the induction of MAA synthesis is a pterin with a distinct absorption peak at 310 nm in one cyanobacterial strain (Portwich and Garcia-Pichel 2000). Biosynthetic pathways of MAA synthesis have now been reported (Balskus and Walsh 2010; Gao and Garcia-Pichel 2011).

High levels of MAAs accumulate in cyanobacterial cells of hypersaline environments (Oren 1997), suggesting they could function as compatible solutes in osmoprotection; but this role, while suggested by the author, can only be minor in comparison to that of known compatible solutes in the same cells, the concentration of which may be very much higher.

MAAs and scytonemin are absent in many cyanobacteria (e.g. *Fischerella* [=*Mastigocladus*], *Synechococcus* spp. and many *Leptolyngbya* [=*Phormidium*]) types from hot springs, as well as in vertically migrating types in soft microbial mats, and from many others in the Culture Collection of Microorganisms from Extreme Environments (CCMEE) at the University of Oregon (Castenholz and Garcia-Pichel 2000 and Castenholz, unpublished data) and in the Pasteur Culture Collection. It is these that must have other means of tolerating UVR or avoiding it. In the case of exposure to full solar irradiance, without any possibility of escape because of various features of the habitat, it is apparent that only efficient repair mechanisms can make up for damage done during daylight hours of clear skies with summer insolation at temperate latitudes (Miller et al. 1998). Most repairs probably take place during darkness or during periods of low light as in morning or before dusk. Cyanobacteria are known to have a very efficient daytime photoreactivation system as compared to *Escherichia coli* (Castenholz and Garcia-Pichel 2000). There is, however, little known of UVR effects and tolerance capability outside of the laboratory, with the exception of papers on cyanobacteria in hot springs (Miller et al. 1998; Dillon et al. 2003; Norris et al. 2002). Although some dinoflagellates have the ability to swim vertically out of the damaging intensities of UVB, this is not true of the marine planktonic cyanobacteria that depend on vertical circulation. Gas-vesiculate cyanobacteria in oceanic waters of the tropics and sub-tropics (e.g. *Trichodesmium*) may circulate to great depths, but in very calm conditions may rise to near the surface and become exposed to detrimental UVR.

19.5.2 UVA

UVA may have both direct and indirect effects on cyanobacteria and algae. NAD(P)H (component cofactor in energy metabolism of anoxygenic and oxygenic phototrophs) and other essential nucleotides with absorption maxima at ~340 nm may be regarded as direct targets of UVA. UVA also has some of the same effects as UVB but with less consequence. Pterines can be additional targets or sensitizers. UVA radiation affects many phenomena negatively, but the exact mechanism is not often known. UVA photooxidative damage primarily involves the guanine components of DNA as a result of singlet oxygen generation (Ravanat et al. 2001), which necessitates a photosensitizing compound. Photosynthesis, growth rate and chlorophyll synthesis are negatively affected by UVA. However, the main effects may be through the production of reactive oxygen that may also be produced by the violet/blue wavelengths if the intensity is sufficiently high. The products are singlet oxygen ($^1O_2$), peroxy radicals, and free radical reactions such as the production of OH• (see Asada and Takahashi 1987). Targets of oxidative damage include unsaturated lipids such as phospholipids (Girotti 2001).

UVA (with UVB excluded) resulted in decreases in photosynthetic rate in various cyanobacteria, such as thermophilic *Synechococcus* (Miller et al. 1998), marine *Oscillatoria* and *Spirulina* (Kruschel and Castenholz 1998), Antarctic *Oscillatoria* (Nadeau et al. 1999), and thermophilic *Mastigocladus* (*Fischerella*) (Castenholz, unpublished data) all in outdoor experiments in which the effects of visible irradiance alone, vis+UVA, and vis+UVA and B were compared. The specific targets of these UVA effects have not been investigated.

Photosynthetic prokaryotes may prevent or alleviate the various detrimental effects of UVA (320–400 nm) and short wavelength visible radiation (400–~500 nm) by synthesizing or maintaining a high carotenoid content which may act as an effective antioxidant or "quencher" of reactive oxygen. This may inhibit lipid peroxidation, and thus stabilize membranes (Britton 1995; Niyogi 1999). A high photon flux in excess of what can be used in the photosynthetic reaction may still be absorbed by tetrapyrroles (e.g. chlorophylls and phycobilins) and will result at least in triplet chlorophyll (^{3}Chl) and resultant $^1O_2$ production. Specific carotenoids (e.g. myxoxanthophyll, echinenone, zeaxanthin) may be effective through the thermal dissipation of excitation energy of chlorophyll and singlet oxygen. Recent evidence shows that singlet oxygen may be quenched by carotenoid-cyclodextrin complexes (Kanofsky and Sima 2009). It is probable that a high ratio of effective carotenoids to photosensitizer (i.e. tetrapyrroles) may be extremely important, particularly at suboptimal temperatures when repair and synthetic processes are slow (see Castenholz and Garcia-Pichel 2000). The protective xanthophyll cycle occurs in eukaryotes *in vivo*, but not in prokaryotic phototrophs (Josue and Frank 2002). Zeaxanthin alone, however, may be sufficient for some degree of photoprotection in cyanobacteria (Niyogi 1999). One of the most conspicuous aspects of high light intensity regimes in natural communities of photosynthetic prokaryotes (e.g. hot spring mats) is the yellow or orange colouration in summer in regions of high light intensity with a very high ratio of carotenoids to chlorophyll and phycobilins (Norris et al. 2002; Vincent et al. 1993). However, the effect of carotenoids as a UVR screen is minimal, since almost all of carotenoid absorption is in the violet/blue/green region of the visible spectrum in prokaryotes. Carotenoids, will absorb these wavelengths and be of great benefit directly under high solar intensity. In some cases certain carotenoids may function mainly as major or partial light harvesting complexes, although this is the case mainly in anoxygenic phototrophic bacteria and various algae (e.g. diatoms, chrysomonads, dinoflagellates)(Castenholz and Garcia-Pichel 2000).

Superoxide radical anions are also produced with high light intensity. For example, increased synthesis of Mn SOD above constitutive levels of Fe SOD may occur in cyanobacteria (Castenholz and Garcia-Pichel 2000). H_2O_2, a product of SOD activity, is considered to be relatively harmless compared to superoxide. In *Synechocystis* PCC 6803, peroxide decomposition is catalyzed by catalase-peroxidase and a thiol-specific peroxidase (Tichy and Vermaas 1999). Tocopherols, ascorbates, and glutathione are also used as peroxide detoxifying compounds (Niyogi 1999).

An important preventative and passive method of protection from UVA results from the presence of scytonemin in the sheath or EPS of cyanobacteria, but this does not apply to all cyanobacteria. Only those that possess some type of EPS and are commonly exposed to UVR (even low intensity UVR) synthesize scytonemin. This includes numerous surface layers of microbial mats in flats infrequently covered by tidal waters (Cockell and Rothschild 1999; Fleming et al. 2007), lower temperature (<~50°C) hot spring mats (Brenowitz and Castenholz 1997; Dillon et al. 2003), terrestrial mats and crusts (Garcia-Pichel and Belnap 1996), shallow and clear oligotrophic fresh waters (Johnson and Castenholz 2000), cyanolichens (Büdel et al. 1997) and many other exposed habitats (Garcia-Pichel and Castenholz 1991; Castenholz and Garcia-Pichel 2000). Scytonemin, as mentioned earlier, has major absorption peaks at ~250 and 370–372 nm (*in vivo*). It is a unique dimeric indole alkaloid with a molecular weight of 544 (Proteau et al. 1993). In mature surface filaments of cyanobacteria scytonemin-rich sheaths may screen out >95% of the UVA and a substantial portion of UVB (see above). This passive method of preventing or slowing the inhibition caused by UVA radiation apparently results in great benefits in terms of fitness and survival, particularly in habitats where desiccation or suboptimal growth conditions prevail (Garcia-Pichel et al. 1992;

Brenowitz and Castenholz 1997; Dillon et al. 2003; Dillon and Castenholz 2003).

The synthesis of scytonemin is initiated and sustained by exposure to UVA although violet/blue wavelengths have some effect (Garcia-Pichel and Castenholz 1991), but some rock-inhabiting cyanobacteria synthesize a small content of scytonemin constitutively (Castenholz, unpublished data). Stresses such as increased temperature and photooxidative conditions, in conjunction with UVA, caused a small increase in scytonemin production in one species of *Chroococcidiopsis* (Dillon et al. 2002). In addition, a moderate osmotic stress, without UVR or blue light, resulted in some scytonemin synthesis. Periodic desiccation in addition to UVA exposure also increased scytonemin content (Fleming and Castenholz 2007). It has been shown that the content of scytonemin per unit area in intertidal *Lyngbya* cf. *aestuarii* increased during the higher solar irradiance period of summer (Karsten et al. 1998). Another stress that promoted the synthesis of scytonemin is diazotrophic growth, a condition that could be considered a stress because of the high energy requirement for N_2-fixation (Fleming and Castenholz 2008). In this case, *Nostoc* ATCC 29133 produced scytonemin under UVA radiation only when no combined nitrogen was available.

The genetic analyses of a scytonemin-less *Nostoc punctiforme* ATCC 29133 mutant (Soule et al. 2007), have opened the door in recent years to the study of the molecular basis of scytonemin biology. Much has been accomplished in this respect in a short time. The mutant implicated a genomic region containing 18 contiguous genes in the synthesis of scytonemin. Similar regions have been since found by comparative genomics or by direct sequencing in a variety of other cyanobacteria (Sorrels et al. 2009; Soule et al. 2009a). Homologous regions in non-heterocystous strains (*Lyngbya* and *Cyanothece*) contain 5 additional genes in the cluster (Soule et al. 2009a). These are also conserved in *Nostoc* and other heterocystous cyanobacteria, where they are non-contiguous. Most of the genes in the upstream region of the *Nostoc* cluster, with the exception of *scyA* and *scyB* that code for novel proteins without an easily predictable function, but a transposon inserted in *scyD* effectively eliminated scytonemin biosynthesis under otherwise inducing conditions. Balskus and Walsh (2008) could subsequently show that the protein coded for in one of these genes (*scy*A) catalyzed the condensation of phenol- and indole-pyruvate moities, a fact that is in agreement with the expected scytonemin synthetic pathway, and with the pyruvate-condensing activity predicted for s*cy*A on the basis of sequence similarity. The functions of most of the other upstream genes have not been clarified, but tentative assignments on the basis of comparative genomics have been carried out for some (Soule et al. 2009a). Downstream in the cluster, one finds redundant orthologs of genes coding for enzymes in the aromatic amino acid pathway. Those present suffice to lead to *p*-hydroxyphenyl-pyruvate from end products of the shikimic acid pathway. Redundant copies of the genes coding for the key regulatory and rate-limiting enzymes of the shikimic acid pathway are found downstream as well. Thus, it seems that the downstream region is dedicated to the delivery of monomeric blocks for scytonemin synthesis. Additionally, two genes immediately upstream from the scytonemin-associated cluster likely encode a two-component sensor kinase and response regulator, respectively. These also are highly conserved in sequence and location among cyanobacterial strains that possess the scytonemin cluster, and may be involved in regulating the expression of the scytonemin-related genes. As expected the expression of all genes in the cluster is positively regulated by exposure to UVA, and transcription proceeds in an operon-like fashion as a single transcript (Soule et al. 2009b). In recent years, much has been learned about the biosynthesis of scytonemin, although it is uncertain in what form it is transported or assembled in the sheath or EPS. Since *scy*D, *scy*E, and *scy*F, have export signal domains, and others have putative transmembrane domains, it can be inferred that scytonemin biosynthesis is compartmentalized within the cell, and that monomer synthesis and initial condensation are cytoplasmic. Later reactions are predicted to be periplasmic (Soule et al. 2009a) (Fig. 19.9).

As an aside, it appears that an unknown compound is present in many marine and freshwater green macro- and micro-algae that acts an UVA and UVB shield with a relatively high protective efficiency (Pescheck et al. 2010). In the case of green freshwater micro-algae there appear to be macromolecules (possibly sporopollenin-like compounds, i.e. algenans) bound to the cell walls.

19.6 Behavioural Methods of Escaping UVR Exposure

Although much is known about vertical movements and regulation of buoyant or semi-buoyant gas-vacuolate cyanobacteria, and anoxygenic phototrophic bacteria in the water column of lakes (Walsby 1994), work that focuses on the effects of the UV portion of the spectrum is lacking.

Gliding filamentous cyanobacteria (as well as a few species of unicellular forms) often move vertically in soft microbial mats and sediments in response to high intensity visible light and UVR (for a summary, see Castenholz and Garcia-Pichel 2000). The downward movement of filamentous cyanobacteria (0.4–>1 mm) in dense microbial mats has been shown to be a response to high solar irradiance, particularly UVR, both UVB and UVA in temperate habitats, hot springs, and cold Antarctic ponds (Garcia-Pichel et al. 1994; Ramsing and Prufert-Bebout 1994; Bebout and Garcia-Pichel 1995; Kruschel and Castenholz 1998; Richardson and Castenholz 1987; Nadeau et al. 1999) (Fig. 19.10). In general, the return towards or to the mat surface occurred in darkness or in dim daylight until UVR

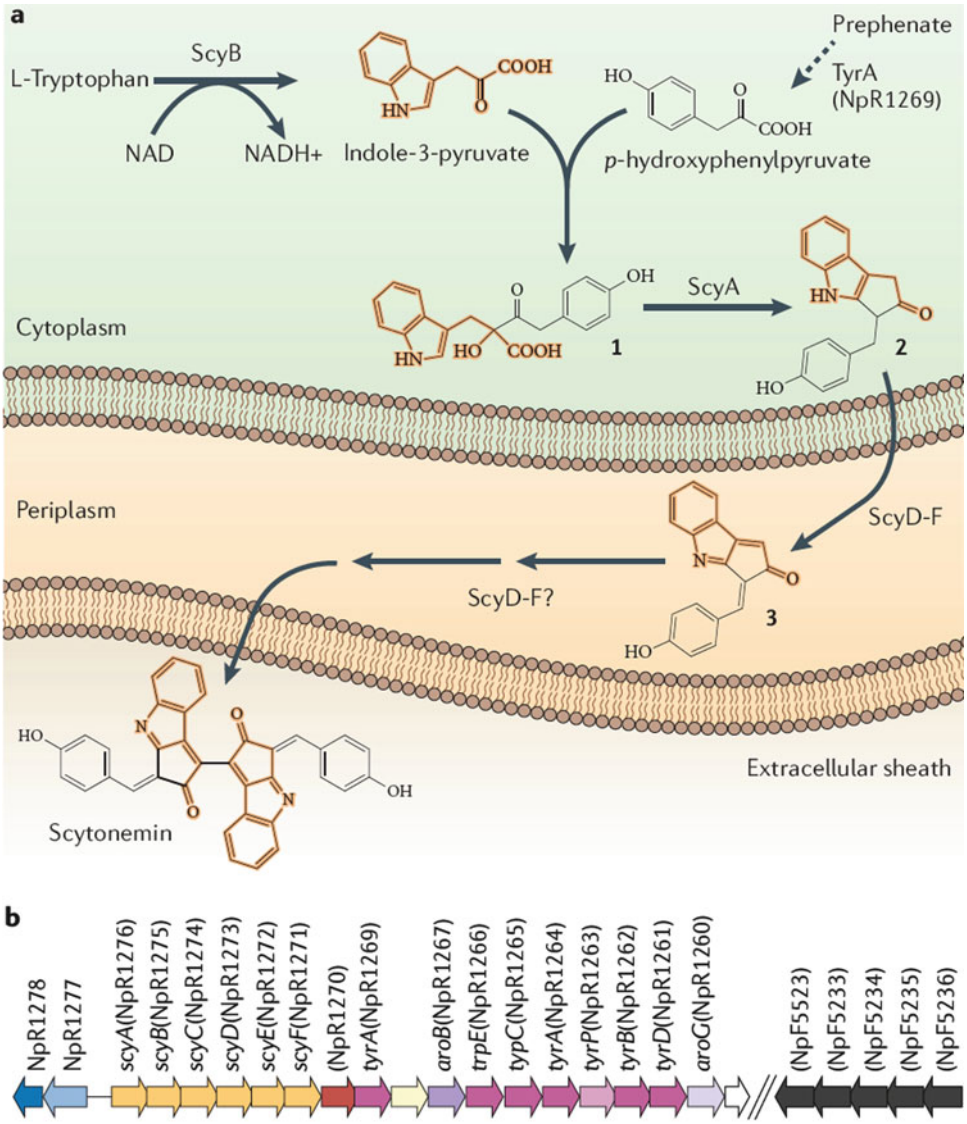

Fig. 19.9 Working model of scytonemin biosynthesis in *Nostoc punctiforme* based on genomic and enzymological analyses: UVA is absorbed and activates the genes in the scytonemin operon (**b**), the gene products of which catalyze the sequence of reactions depicted in (**a**), likely in a compartimentalized fashion. The genes in purple color constitute redundant orthologs of key shikimic acid and aromatic amino acid biosynthetic pathways. (From Gao and Garcia-Pichel 2011, Fig. 3, p 795. Courtesy of Nature Publishing Company)

or high visible light intensities again appear to stop the upward movement (Garcia-Pichel et al. 1994; Kruschel and Castenholz 1998). In two cases it has been shown that failure to migrate downward from the surface during periods of high solar irradiance (including UVR) would have resulted in extreme inhibition of photosynthesis or death (Garcia-Pichel et al. 1994; Kruschel and Castenholz 1998). Filamentous and unicellular cyanobacteria have also been shown to move vertically in soft hot spring mats, also as a response to high light intensity, but UVR was not specifically taken into account (Castenholz 1968; Richardson and Castenholz 1987; Ramsing et al. 1997). In almost all of the cases cited, the cyanobacteria involved did not possess MAAs nor did they have the ability to withstand large doses of UVR. Thus, escape was essentially the only tactic for survival. Garcia-Pichel et al. (1994) have also shown in one case, by the use of micro light sensors, that the gradual descent of *Spirulina* and *Oscillatoria* to ~0.5 mm and later the ascent in a soft hypersaline mat would result in maximum photosynthetic rates during most daylight hours. Thus, the daytime descent may not be simply an escape but a finely regulated optimization of light available for photosynthesis. These cyanobacteria also retained high cellular contents of chlorophyll *a* and phycocyanin. Retaining this condition would be distinctly advantageous during overcast periods of low light intensity and during early morning and late afternoon when these cyanobacteria would be at the mat surface and able to absorb the low photon flux more efficiently for

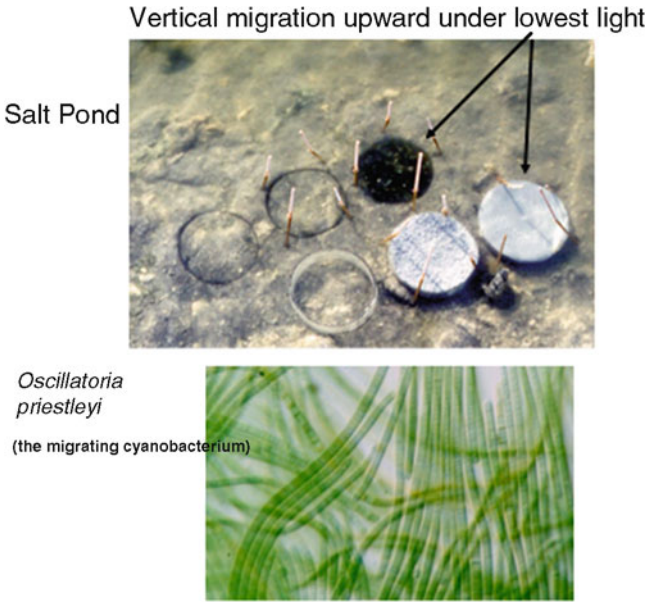

Fig. 19.10 Upward migration of *Oscillatoria* cf. *priestleyi* in hypersaline "Salt Pond" (Bratina Island area, Antarctica), under the lowest light intensity with filter removed after 4 h of treatment (*upper right dark area*). The intensity was ~5–8 Wm^{-2} of PAR with no detectable UVR, and the temperature 6–8°C. The same result occurred under darkness, but not under ~12–20 Wm^{-2} (*next filter to left*) where UVA was barely measurable, or under full solar radiation (230–360 Wm^{-2}) last ring to *left*. A more intricate series of experiments (also in "Salt Pond") are described by Nadeau et al. (1999). The rate of movement was about 50% slower than that observed for motile cyanobacteria in temperate mats in Baja California (Kruschel and Castenholz 1998). *Oscillatoria* cf. *priestleyi* (~7 μm trichome diameter) is shown in the lower panel (Photos by RWC)

photosynthetic activity. A high content of chlorophyll and/or phycocyanin could also become a detriment and act as photosensitizers if the cells were suddenly exposed to high solar irradiance. In more sedentary cyanobacteria the synthesis of these pigments are regulated downward by stopping synthesis or by regulated degradation, thus increasing the ratio of carotenoids to photosensitizers, allowing an increased tolerance to photo-oxidative stress.

19.7 Effects of Decrease of UVR on Phototrophic Communities

Bothwell et al. (1993, 1994) studied the effects of 3–5 weeks of UVR applied to a lotic community that colonized an artificial substrate. As a result of enhanced UVB a greater biomass of diatoms accumulated than in the control. However, chironomid larvae that normally graze on diatoms were more sensitive than the diatoms to UVB. Since these were indoor experiments the +UV treatment may be closer to natural field conditions than those of the controls. Epiphytic cyanobacterial mats from tropical mangrove communities were subjected to +UV and -UV treatments for 27 days with laboratory

Table 19.1 Multiple methods of tolerating UV radiation by cyanobacteria (From Castenholz 2004, Table 1, p 457. With kind permission from Springer Science + Business Media B.V.)

Method	A	B	C
Scytonemin	Yes	No	No
MAAs	Most yes	Many yes	Many yes
Motility-avoidance	No	Yes	No
Chlorophyll-phycobilin-carotenoid regulation	Yes	Yes	Yes
Carotenoid quenching	Yes	Yes	Yes
SOD, peroxidase, etc.	Yes	Yes	Yes
Repair – synthesis	Yes	Yes	Yes

A sheathed types, B motile types (filamentous & unicellular), C no motility, sheath or EPS. Motile hormogonial stages of type A may avoid UVR

UVB+UVA+PAR, UVA+PAR, or PAR only. Large differences in species arrangement and abundance occurred (Sheridan 2001). With UVA and UVB the top layer of scytonemin-containing, diazotrophic *Nostoc* cf. *commune* and *Scytonema* sp. were maintained as in the natural mat. When UVR was excluded, the *Nostoc* was overrun or overgrown by a less UV-tolerant species of *Phormidium* which was not capable of diazotrophy. As a result, overall N_2-fixation decreased greatly.

Two alkaline geothermal streams in Yellowstone National Park (40–47°C) were covered for 1–3 months with filters that excluded or transmitted UVR (Norris et al. 2002). There were no apparent cyanobacterial community composition changes during the summer with or without high or low UVR, as assessed by DGGE (denaturing gradient gel electrophoresis). Although the cyanobacterial composition of these communities was apparently stable, surface layers of cyanobacteria protected by filters from UV radiation were not as competent photosynthetically as those that had been maintained under UVR. This decrease in competence was expressed as a temporary loss of the ability to perform at a maximum rate under full solar irradiance (including UVR). Recovery occurred within a week under full irradiance.

19.8 Conclusions

UV radiation effects on microbial populations have been studied in recent years with increasing frequency and with refined molecular methodology. One reason is the awareness of decreasing levels of ozone in the stratosphere in some regions that result in increased UVB flux. Microbial populations may exhibit a more immediate and measurable sensitivity to small increases in UVR than larger macrophytes and metazoans that may require weeks, months, or years to show UVR effects. Some cyanobacteria, representing descendants of the oldest oxygenic inhabitants of the planet, have evolved many methods (or strategies) for coping with present levels of UVR (Table 19.1).

Since cyanobacteria have invaded (or remain as relics) in a large number of extreme environments, including shallow water and terrestrial surfaces, they currently must often cope with high solar irradiance in which UVR can be the most detrimental factor. They have done so by evolving sunscreen pigments that envelope the cells and work even when cells are at rest, and by synthesizing other compounds such as mycosporine-like amino acids (the true value of which is still not completely evaluated). Also, they have probably evolved several efficient methods of dissipating excess photon energy, and by using regulated systems for repair of damaged DNA and for replacement of UV damaged compounds, and by using directed, "phototactic" gliding motility in soft microbial mats or sediments for escaping the daytime high intensities of solar irradiance.

Acknowledgements RWC is very grateful to the US National Science Foundation, which for over many years has supported research on UV effects on cyanobacteria.

References

Asada K, Takahashi M (1987) Production and scavenging of active oxygen in photosynthesis. In: Kyle DJ, Osmond CB, Arntzen CJ (eds) Photoinhibition. Elsevier Science Publishers, Amsterdam, pp 227–287

Bailey S, Grossman A (2008) Photoprotection in cyanobacteria: regulation of light harvesting. Photochem Photobiol 84:1410–1420

Balskus EP, Walsh CT (2008) Investigating the initial steps in the biosynthesis of cyanobacterial sunscreen scytonemin. J Am Chem Soc 130:15260–15261

Balskus EP, Walsh CT (2010) The genetic and molecular basis of sunscreen biosynthesis in cyanobacteria. Science 329:1653–1656

Bebout BM, Garcia-Pichel F (1995) UVB-induced vertical migrations of cyanobacteria in a microbial mat. Appl Environ Microbiol 61:4215–4222

Billi D, Friedmann EI, Hofer KG, Caiola MG, Ocampo-Friedmann R (2000) Ionizing-radiation resistance in the desiccation-tolerant cyanobacterium *Chroococcidiopsis*. Appl Environ Microbiol 66:1489–1492

Bonilla SE, Villeneuve V, Vincent WF (2005) Benthic and planktonic algal communities in a High Arctic lake: pigment structure and contrasting responses to nutrient enrichment. J Phycol 41:1120–1130

Booth CR, Morrow JH (1997) The penetration of UV into natural waters. Photochem Photobiol 65:254–257

Bothwell ML, Sherbot D, Roberg AC, Daley RJ (1993) Influence of natural ultraviolet radiation on lotic periphytic diatom community growth, biomass accrual, and species composition: short-term versus long-term effects. J Phycol 29:24–35

Bothwell ML, Sherbot DMJ, Pollock CM (1994) Ecosystem response to solar ultraviolet-B radiation: influence of trophic level interactions. Science 265:97–100

Bouchard JN, Roy S, Ferreyra G, Campbell DA, Curtosi A (2005) Ultraviolet-B effects on photosystem II efficiency of natural phytoplankton communities from Antarctica. Polar Biol 28:607–618

Brenowitz S, Castenholz RW (1997) Long-term effects of UV and visible irradiance on natural populations of a scytonemin-containing cyanobacterium (*Calothrix* sp.). FEMS Microbiol Ecol 24:343–352

Britton G (1995) Structure and properties of carotenoids in relation to function. FASEB J 9:1551–1558

Büdel B, Karsten U, Garcia-Pichel F (1997) Ultraviolet-absorbing scytonemin and mycosporine-like amino acid derivatives in exposed, rock-inhabiting cyanobacterial lichens. Oecologia 112:165–172

Campbell D, Eriksson M-J, Öquist G, Gustafsson P, Clarke AK (1998) The cyanobacterium *Synechococcus* resists UV-B by exchanging photosystem II reaction center D1 proteins. Proc Natl Acad Sci USA 95:364–369

Castenholz RW (1968) The behavior of *Oscillatoria terebriformis* in hot springs. J Phycol 4:132–139

Castenholz RW (2004) Phototrophic bacteria under UV stress. In: Seckbach J (ed) Origins, evolution and biodiversity of microbial life. Kluwer Academic Publishers, Dordrecht, pp 445–461

Castenholz RW (2009) Mats, microbial. In: Encyclopedia of Microbiology, Elsevier, pp 278–292

Castenholz RW, Garcia-Pichel F (2000) Cyanobacterial responses to UV-radiation. In: Whitton BA, Potts M (eds) The ecology of cyanobacteria. Their diversity in time and space. Kluwer Academic Publishers, Dordrecht, pp 591–611, 669 pp

Castenholz RW, Schneider A (1993) Cyanobacterial dominance at high and low temperatures: optimal conditions or precarious existence? In: Guerrero R, Pedros-Alio C (eds) Trends in microbial ecology. Spanish Society for Microbiology, Barcelona, pp 19–24

Choi J-S, Chung Y-H, Moon Y-J, Kim C, Watanabe M, Song P-S, Joe C-O, Bogorad L, Park YM (1999) Photomovement of the gliding cyanobacterium *Synechocystis* sp. PCC 6803. Photochem Photobiol 70:95–102

Cockell CS (1998) The biological effects of high ultraviolet radiation on early Earth: a theoretical evaluation. J Theor Biol 193:717–729

Cockell CS (2001) A photobiological history of Earth. In: Cockell CS, Blaustein AR (eds) Ecosystems, evolution, and ultraviolet radiation. Springer, New York, pp 1–35, 221 pp

Cockell CS, Rothschild LJ (1999) The effects of UV radiation A and B on diurnal variation in photosynthesis in three taxonomically and ecologically diverse microbial mats. Photochem Photobiol 69:203–210

Cullen JJ, Neale PJ (1994) Ultraviolet radiation, ozone depletion and marine photosynthesis. Photosynth Res 39:303–320

Day TA, Neale PJ (2002) Effects of UV-B radiation on terrestrial and aquatic primary producers. Annu Rev Ecol Syst 33:371–396

Des Marais DJ (1995) The biogeochemistry of hypersaline microbial mats. Adv Microbiol Ecol 14:251–274

Diffey BL, Green AT, Loftus MJ, Johnson GJ, Lee PS (1995) A portable instrument for measuring ground reflectance in the ultraviolet. Photochem Photobiol 61:68–70

Dillon JG, Castenholz RW (1999) Scytonemin, a cyanobacterial sheath pigment, protects against UVC radiation: implications for early photosynthetic life. J Phycol 35:673–681

Dillon JG, Castenholz RW (2003) The synthesis of the UV-screening pigment, scytonemin, and photosynthetic performance in isolates from closely related natural populations of cyanobacteria (*Calothrix* sp.). Environ Microbiol 5:484–491

Dillon JG, Tatsumi CM, Tandingan PG, Castenholz RW (2002) Effect of environmental factors on the synthesis of scytonemin, a UV-screening pigment, in a cyanobacterium (*Chroococcidiopsis* sp.). Arch Microbiol 177:322–331

Dillon JG, Miller SR, Castenholz RW (2003) UV-acclimation responses in natural populations of cyanobacteria (*Calothrix* sp.). Environ Microbiol 5:473–483

Dodds WK, Castenholz RW (1988) The biological effects of nitrate fertilization and water replacement in an oligotrophic cold water pond. Hydrobiologia 162:141–146

Eguchi M, Oketa T, Miyamoto N, Maeda H, Kawai A (1996) Occurrence of viable photoautotrophic picoplankton in the aphotic zone of Lake Biwa, Japan. J Plankton Res 18:539–550

Ehling-Schulz M, Scherer S (1999) UV protection in cyanobacteria. Eur J Phycol 34:329–338

Ehling-Schulz M, Bilger W, Scherer S (1997) UV-B-induced synthesis of photoprotective pigments and extracellular polysaccharides in the terrestrial cyanobacterium *Nostoc commune*. J Bacteriol 179:1940–1945

Fleming ED, Castenholz RW (2007) Effects of periodic desiccation on the synthesis of the UV-screening compound, scytonemin, in cyanobacteria. Environ Microbiol 9:1448–1455
Fleming ED, Castenholz RW (2008) Effects of nitrogen source on the synthesis of the UV-screening compound, scytonemin, in the cyanobacterium *Nostoc punctiforme* PCC 73102. FEMS Microbiol Ecol 63:301–308
Fleming ED, Bebout BM, Castenholz RW (2007) Effects of salinity and light intensity on the resumption of photosynthesis in a rehydrated cyanobacterial mat from Baja California Sur, Mexico. J Phycol 43:15–24
Frederick JE, Snell HE, Haywood EK (1989) Solar ultraviolet radiation at the earth's surface. Photochem Photobiol 50:443–450
Gao K, Ye C (2007) Photosynthetic insensitivity of the terrestrial cyanobacterium *Nostoc flagelliforme* to solar UV radiation while rehydrated or desiccated. J Phycol 43:628–635
Gao K, Li P, Watanabe T, Heibling EW (2008) Combined effects of ultraviolet radiation and temperature on morphology, photosynthesis, and DNA of *Arthrospira (Spirulina) platensis* (Cyanophyta). J Phycol 44:777–786
Gao Q, Garcia-Pichel F (2011) Microbial ultraviolet sunscreens. Nat Rev Microbiol 9:791–802
Garcia-Pichel F (1994) A model for internal self-shading in planktonic microorganisms and its implications for the usefulness of sunscreens. Limnol Oceanogr 39:1704–1717
Garcia-Pichel F (1998) Solar ultraviolet and the evolutionary history of cyanobacteria. Orig Life Evol Biosph 28:321–347
Garcia-Pichel F, Bebout BM (1996) The penetration of ultraviolet radiation into shallow water sediments: high exposure for photosynthetic communities. Mar Ecol Prog Ser 131:257–262
Garcia-Pichel F, Belnap J (1996) Microenvironments and microscale productivity of cyanobacterial desert crusts. J Phycol 32:774–782
Garcia-Pichel F, Castenholz RW (1991) Charaterization and biological implications of scytonemin, a cyanobacterial sheath pigment. J Phycol 27:395–409
Garcia-Pichel F, Castenholz RW (1993) Occurrence of UV-absorbing, mycosporine-like compounds among cyanobacterial isolates and an estimate of their screening capacity. Appl Environ Microbiol 59:163–169
Garcia-Pichel F, Sherry ND, Castenholz RW (1992) Evidence for an ultraviolet sunscreen role of the extracellular pigment scytonemin in the terrestrial cyanobacterium *Chlrogloeopsis* sp. Photochem Photobiol 56:17–23
Garcia-Pichel F, Wingard CE, Castenholz RW (1993) Evidence regarding the UV-sunscreen role of a mycosporine-like compound in the cyanobacterium *Gloeocapsa* sp. Appl Environ Microbiol 59:170–176
Garcia-Pichel F, Mechling M, Castenholz RW (1994) Diel migrations of microorganisms within a benthic, hypersaline mat community. Appl Environ Microbiol 60:1500–1511
Gieskes WWC, Buma AGJ (1997) UV damage to plant life in a photobiologically dynamic environment: the case of marine phytoplankton. Plant Ecol 128:16–25
Gill RT, Katsoulakis E, Schmitt W, Taroncher-Oldenburg G, Misra J, Stephanopoulos G (2002) Genome-wide dynamic transcriptional profiling of the light-to-dark transition in *Synechocystis* sp. strain PCC 6803. J Bacteriol 184:3671–3681
Girotti AW (2001) Photooxidized oxidation of membrane lipids: reaction pathways, cytotoxic effects, and cytoprotective mechanisms. J Photochem Photobiol B 63:103–113
Häder D-P (1984) Effects of UV-B on motility and photoorientation in the cyanobacterium, *Phormidium uncinatum*. Arch Microbiol 140:34–39
Häder D-P (2001) Ultraviolet radiation and aquatic microbial ecosystems. In: Cockell CS, Blaustein AR (eds) Ecosystems, evolution, and ultraviolet radiation. Springer, New York, pp 150–169
Häder D-P, Lebert M, Schuster M, Del Ciampo L, Helbling EW, McKenzie R (2007) ELDONET-a decade of monitoring solar radiation on five continents. Photochem Photobiol 83:1348–1357
He Y-Y, Klisch M, Häder D-P (2002) Adaptation of cyanobacteria to UV-B stress correlated with oxidative stress and oxidative damage. Photochem Photobiol 76:188–196
Helbling EW, Villafañe V, Holm-Hansen O (1994) Effects of ultraviolet radiation on Antarctic marine plankton photosynthesis with particular attention to the influence of mixing. In: Weiler CS, Penhale PA (eds) Ultraviolet radiation in Antarctica: measurements and biological effects, vol 62. American Geophysical Union, Washington, DC, pp 207–227
Hockberger PE (2002) A history of ultraviolet photobiology for humans, animals and microorganisms. Photochem Photobiol 76:561–579
Holm-Hansen O, Lubin D, Helbling EW (1993) Ultraviolet radiation and its effects on organisms in aquatic environments. In: Young AR, Björn LO, Moan J, Nultsch W (eds) Environmental UV photobiology. Plenum Press, New York, pp 379–425
Hren MT, Tice MM, Chamberlain CP (2009) Oxygen and hydrogen isotope evidence for a temperate climate 3.42 billion years ago. Nature 462:205–208
Jägger J (1985) Solar-UV action on living cells. Praeger, New York
Javor BJ, Castenholz RW (1981) Laminated microbial mats, Laguna Guerrero Negro, Mexico. Geomicrobiology 2:237–273
Javor BJ, Castenholz RW (1984) Productivity studies of microbial mats, Laguna Guerrero Negro, Mexico. In: Cohen Y, Castenholz RW, Halvorson HO (eds) Microbial mats: stromatolites. Alan R. Liss, Inc., New York, pp 149–170
Jeffrey WH, Pledger RJ, Aas P, Hager S, Coffin RB, Von Haven R, Mitchell DL (1996) Diel and depth profiles of DNA photodamage in bacterioplankton exposed to ambient solar ultraviolet radiation. Mar Ecol Prog Ser 137:283–291
Johnson AC, Castenholz RW (2000) Preliminary observations of the benthic cyanobacteria of Waldo Lake and their potential contribution to lake productivity. Lake Reserv Manag 16:85–90
Josue JS, Frank HA (2002) Direct determination of the S_1 excited-state energies of xanthophylls by low-temperature fluorescence spectroscopy. J Phys Chem A 106:2815–2824
Kanofsky JR, Sima PD (2009) Quenching of singlet oxygen by a carotenoid-cyclodextrin complex: the importance of aggregate formation. Photochem Photobiol 85:391–399
Karlsson J, Byström P, Ask J, Ask P, Persson L, Jansson M (2009) Light limitation of nutrientpoor lake ecosystems. Nature 460:506–509
Karsten U, Maier J, Garcia-Pichel F (1998) Seasonality in UV-absorbing compounds of cyanobacterial mat communities from an intertidal mangrove. Aquat Microb Ecol 16:37–44
Kasting JF (1987) Theoretical constraints on oxygen and carbon dioxide concentrations in the Precambrian atmosphere. Precambrian Res 34:205–229
Kasting JF, Zahnle KJ, Pinto JP, Young AT (1989) Sulfur, ultraviolet radiation, and the early evolution of life. Orig Life Evol Biosph 19:95–108
Kelman D, Ben-Amotz A, Berman-Frank I (2009) Carotenoids provide the major antioxidant defence in the globally significant N_2-fixing marine cyanobacterium *Trichodesmium*. Environ Microbiol 11:1897–1908
Knoll AH (2008) Cyanobacteria and earth history. In: Herrero A, Flores E (eds) The cyanobacteria – molecular biology, genomics and evolution. Caister Academic Press, Norfolk, pp 1–19, 484 pp
Koller LR (1965) Ultraviolet radiation. Wiley, New York, 312 pp
Kruschel C, Castenholz RW (1998) The effect of solar UV and visible irradiance on the vertical movements of cyanobacteria in microbial mats of hypersaline waters. FEMS Microbiol Ecol 27:53–72
Kvalevåg MM, Myhre G, Lund Myhre CE (2009) Extensive reduction of surface UV radiation since 1750 in world's populated regions. Atmos Chem Phys 9:7737–7751
Lao K, Glazer AN (1996) Ultraviolet-B photodestruction of a light-harvesting complex. Proc Natl Acad Sci USA 93:5258–5263
Laurion I, Roy S (2009) Growth and photoprotection in three dinoflagellates (including two strains of *Alexandrium tamarense*)

and one diatom exposed to four weeks of natural and enhanced ultraviolet-B radiation. J Phycol 45:16–33

Lehr CR, Frank SD, D'Imperio S, Kalinin A, Toplin JA, Norris TB, Castenholz RW, McDermott TR (2007) Cyanidial (Cyanidiales) population diversity and dynamics in an acid-sulfate chloride spring in Yellowstone National Park. J Phycol 43:3–14

Los DA, Suzuki I, Zinchenko VV, Murata N (2008) Stress responses in *Synechocystis*: regulated genes and regulated systems. In: Herrero A, Flores E (eds) The cyanobacteria – molecular biology, genomics and evolution. Caister Academic Press, Norfolk, pp 117–157, 484 pp

MacDonald TM, Dubois L, Smith LC, Campbell DA (2003) Sensitivity of cyanobacterial antenna, reaction center and CO_2 assimilation transcripts and proteins to moderate UVB: light acclimation potentiates resistance to UVB. Photochem Photobiol 77:405–412

Máté Z, Sass L, Szekeres M, Vass I, Nagy F (1998) UV-B-induced differential transcription of *psbA* genes encoding the D1 protein of photosystem II in the cyanobacterium *Synechocystis* 6803. J Biol Chem 273:17439–17444

Matthes U, Turner SJ, Larson DW (2001) Light attenuation by limestone rock and its constraint on the depth distribution of endolithic algae and cyanobacteria. Int J Plant Sci 162:262–270

Mazor G, Kidron GJ, Vonshak A, Abeliovich A (1996) The role of cyanobacterial exopolysaccharides in structuring desert microbial crusts. FEMS Microbiol Ecol 21:21–130

Meador JA, Baldwin AJ, Catala P, Jeffrey WH, Joux F, Moss JA, Pakulski D, Stevens R, Mitchell DL (2009) Sunlight-induced DNA damage in marine micro-organisms collected along a latitudinal gradient from 70°N to 68°S. Photochem Photobiol 85:412–420

Miller SR, Wingard CE, Castenholz RW (1998) Effects of visible light and UV radiation on photosynthesis in a population of a hot spring cyanobacterium, a *Synechococcus* sp., subjected to high-temperature stress. Appl Environ Microbiol 64:3893–3899

Morel A, Gentili B, Claustrre H, Babin M, Bricaud A, Ras J, Tièche F (2007) Optical properties of the "clearest" natural waters. Limnol Oceanogr 52:217–229

Nadeau T-L, Castenholz RW (2000) Characterization of psychrophilic oscillatorians (Cyanobacteria) from Antarctic meltwater ponds. J Phycol 36:914–923

Nadeau T-L, Howard-Williams H, Castenholz RW (1999) Effects of solar UV and visible irradiance on photosynthesis and vertical migration of *Oscillatoria* sp (cyanobacteria) in an Antarctic microbial mat. Aquat MicrobEcol 20:231–243

Nicholson P, Osborn RW, Howe CJ (1987) Induction of protein synthesis in response to ultraviolet light, nalidixic acid and heat shock in the cyanobacterium *Phormidium laminosum*. FEBS Lett 221:110–114

Nielsen T, Ekelund NGA (1995) Influence of solar ultraviolet radiation on photosynthesis and motility of marine phytoplankton. FEMS Microbiol Ecol 18:281–288

Nienow JA, Friedmann EI (1993) Terrestrial lithophytic (rock) communities. In: Friedmann EI (ed) Antarctic microbiology. Wiley-Liss, New York, pp 343–412

Niyogi KK (1999) Photoprotection revisited: genetic and molecular approaches. Annu Rev Plant Physiol Plant Mol Biol 50:333–359

Norris TB, Castenholz RW (2006) Endolithic photosynthetic communities within ancient and recent travertine deposits in Yellowstone National Park. FEMS Microbiol Ecol 57:470–483

Norris TB, McDermott TR, Castenholz RW (2002) The long-term effects of UV exclusion on the microbial composition and photosynthetic competence of bacteria in hot-spring microbial mats. FEMS Microbiol Ecol 39:193–209

Olsson-Francis K, de la Torre R, Cockell CS et al (2010) Isolation of novel extreme-tolerant cyanobacteria from a rock-dwelling microbial community by using exposure to low Earth orbit. Appl Environ Microbiol 76:2115–2121

Orce VL, Helbling EW (1997) Latitudinal UVR-PAR measurements in Argentina: extent of the "ozone hole". Glob Planet Change 15:113–121

Oren A (1997) Mycosporine-like amino acids as osmotic solutes in a community of halophilic cyanobacteria. Geomicrobiol J 14: 231–240

Pakker H, Martins RST, Boelen P, Buma AGJ, Nikaido O, Breeman AM (2000) Effects of temperature on the photoreactivation of ultraviolet-B-induced DNA damage in *Palmaria palmata* (Rhodophyta). J Phycol 36:334–341

Pavlov AA, Kasting JF (2002) Mass-independent fractionation of sulfur isotopes in Archean sediments: strong evidence for an anoxic Archean atmosphere. Astrobiology 2:27–41

Pescheck F, Bischof K, Bilger W (2010) Screening of ultraviolet-A and ultraviolet-B radiation in marine green macroalgae (Chlorophyta). J Phycol 46:444–455

Phoenix VR, Bennett PC, Engel AS, Tyler SW, Ferris FG (2006) Chilean high-altitude hot spring sinters: a model system for UV screening mechanisms by early Precambrian cyanobacteria. Geobiology 4:15–28

Pierson BK (1994) The emergence, diversification, and role of photosynthetic eubacteria. In: Bengtson S, Bergström J, Vidal G, Knoll A (eds) Early life on earth. Columbia University Press, New York, pp 161–180, 605 pp

Pierson BK, Mitchell HK, Ruff-Roberts AL (1993) *Chloroflexus aurantiacus* and ultraviolet radiation: implications for Archean shallow-water stromatolites. Orig Life Evol Biosph 23:243–260

Porankiewicz J, Schelin J, Clarke AK (1998) The ATP-dependent Clp protease is essential for acclimation to UV-B and low temperature in the cyanobacterium *Synechococcus*. Mol Microbiol 29:275–283

Portwich A, Garcia-Pichel F (1999) Ultraviolet and osmotic stresses induce and regulate the synthesis of mycosporines in the cyanobacterium *Chlorogloeopsis* PCC 6912. Arch Microbiol 172:187–192

Portwich A, Garcia-Pichel F (2000) A novel prokaryotic UVB photoreceptor in the cyanobacterium *Chlorogloeopsis* PCC 6912. Photochem Photobiol 71:493–498

Portwich A, Garcia-Pichel F (2003) Biosynthetic pathway of mycosporines (mycosporine-like amino acids) in the cyanobacterium *Chlorogloeopsis* sp. strain PCC 6912. Phycologia 42:384–392

Postius C, Ernst A, Kenter U, Böger P (1996) Persistence and genetic diversity among strains of the phycoerythrin-rich cyanobacteria from the picoplankton of Lake Constance. J Plankton Res 18: 1159–1166

Potts M (1994) Desiccation tolerance of prokaryotes. Microbiol Rev 58:755–805

Prezelin BB, Boucher NP, Smith RC (1994) Marine primary production under the influence of the Antarctic ozone hole: Icecolors'90. In: Weiler CS, Penhale PA (eds) Ultraviolet radiation in Antarctica: measurement and biological effects, vol 62. American Geophysical Union, Washington, DC, pp 159–186

Proteau PJ, Gerwick WH, Garcia-Pichel F, Castenholz RW (1993) The structure of scytonemin, an ultraviolet sunscreen pigment from the sheaths of cyanobacteria. Experientia 49:825–829

Quesada A, Vincent WF (1997) Strategies of adaptation by Antarctic cyanobacteria to ultraviolet radiation. Eur J Phycol 32:335–342

Ramsing NB, Prufert-Bebout L et al (1994) Motility of *Microcoleus chthonoplastes* subjected to different light intensities quantified by digital image analysis. In: Stal LJ, Caumette P (eds) Microbial mats. Structure, development and environmental significance, vol 35, NATO ASI series. Springer, Berlin, pp 183–191

Ramsing NB, Ferris MJ, Ward DM (1997) Light-induced motility of thermophilic *Synechococcus* isolates from Octopus Spring, Yellowstone National Park. Appl Environ Microbiol 63:2347–2354

Rasmussen B, Blake TM, Fletcher IR, Kilburn MR (2009) Evidence for microbial life in synsedimentary cavities from 2.75 Ga terrestrial environments. Geology 37:423–426

Ravanat J-L, Douki T, Cadet J (2001) Direct and indirect effects of UV radiation on DNA and its components. J Photochem Photobiol B 63:88–102

Richardson LL, Castenholz RW (1987) Diel vertical movements of the cyanobacterium *Oscillatoria terebriformis* in a sulfide-rich hot spring microbial mat. Appl Environ Microbiol 53:2142–2150

Robinson N (1966) Solar radiation. Elsevier, Amsterdam

Roy S (2000) Strategies for the minimization of UV-induced damage. In: de Mora S, Demers S, Vernet M (eds) The effects of UV radiation in the marine environment. Cambridge University Press, Cambridge, pp 176–205

Roy CR, Gies HP, Tomlinson DW, Lugg DL (1994) Effects of ozone depletion on the ultraviolet radiation environment at the Australian stations in Antarctica. In: Weiler CS, Penhale PA (eds) Ultraviolet radiation in Antarctica: measurement and biological effects, vol 62. American Geophysical Union, Washington, DC, pp 1–15

Sancar A (1994) Mechanisms of DNA excision repair. Science 266:1954–1956

Sancar A (1996) No "end of history" for photolyases. Science 272:48–49

Sass L, Spetea C, Máté Z, Nagy F, Vass I (1997) Repair of UVB induced damage of photosystem II via *de novo* synthesis of the D1 and D2 reaction centre subunits in *Synechocystis* sp. PCC 6803. Photosynth Res 54:55–62

Scully NM, McQueen DJ, Lean DRS (1996) Hydrogen peroxide formation: the interaction of ultraviolet radiation and dissolved organic carbon in lake waters along a 43–75°N gradient. Limnol Oceanogr 41:540–548

Sheridan RP (2001) The role of ultraviolet radiation in maintaining the three-dimensional structure of a cyanobacterial mat community and facilitating nitrogen fixation. J Phycol 37:731–737

Shibata H, Katsuya B, Ochiai H (1991) Near-UV irradiation induces shock proteins in *Anacystis nidulans* R-2; possible role of active oxygen. Plant Cell Physiol 32:771–776

Shick JM, Dunlap WC (2002) Mycosporine-like amino acids and related gadusols: biosynthesis, accumulation, and UV-protective functions in aquatic organisms. Annu Rev Physiol 64:223–262

Singh SP, Kumari S, Rostagi RP, Singh KL, Richa SRP (2010) Photoprotective and biotechnical potentials of cyanobacterial sheath pigment, scytonemin. Afr J Biotechnol 9:580–588

Sinha RP, Klisch M, Helbling EW, Häder D-P (2001) Induction of mycosporine-like amino acids (MAAs) in cyanobacteria by solar ultraviolet-B radiation. J Photochem Photobiol B 60:129–135

Smith RC, Baker KS (1981) Optical properties of the clearest natural seawaters. Appl Opt 20:177–188

Sobrino C, Ward ML, Neale PJ (2008) Acclimation to elevated carbon dioxide and ultraviolet radiation in the diatom *Thallasiosira pseudonana*: effects on growth, photosynthesis, and spectral sensitivity of photoinhibition. Limnol Oceanogr 53:494–505

Sorrels CM, Proteau PJ, Gerwick WH (2009) Organization, evolution, and expression analysis of the biosynthetic gene cluster for scytonemin, a cyanobacterial UV-absorbing pigment. Appl Environ Microbiol 75:4861–4869

Soule T, Stout V, Swingley WD, Meeks JC, Garcia-Pichel F (2007) Molecular genetics and genomic analysis of scytonemin biosynthesis in *Nostoc punctiforme* ATCC 29133. J Bacteriol 189:4465–4472

Soule T, Palmer K, Gao Q, Potrafka RM, Stout V, Garcia-Pichel F (2009a) A comparative genomics approach to understanding the biosynthesis of the sunscreen scytonemin in cyanobacteria. BMC Genomics 10:336–345

Soule T, Garcia-Pichel F, Stout V (2009b) Gene expression patterns associated with the biosynthesis of the sunscreen scytonemin in *Nostoc punctiforme* ATCC 29133 in response to UVA radiation. J Bacteriol 191:4639–4646

Tang EPY, Tremblay R, Vincent WF (1997) Cyanobacterial dominance of polar freshwater ecosystems: are high latitude mat formers adapted to low temperature? J Phycol 33:171–181

Tichy M, Vermaas W (1999) In vivo role of catalase-peroxidase in *Synechocystis* sp. strain PCC 6803. J Bacteriol 181:1875–1882

Van Baalen C (1968) The effects of ultraviolet irradiation on a coccoid blue-green alga: survival, photosynthesis, and photoreactivation. Plant Physiol 43:1689–1695

Van Baalen C, O'Donnell K (1972) Action spectra for ultraviolet killing and photoreactivation in the blue-green alga *Agmenellum quadruplicatum*. Photochem Photobiol 15:269–274

Vincent WF (1988) Microbial ecosystems of Antarctica. Cambridge University Press, Cambridge, 304 pp

Vincent WF (2000) Cyanobacterial dominance in the polar regions. In: Whitton BA, Potts M (eds) The ecology of cyanobacteria. Their diversity in time and space. Kluwer Academic Publishers, Dordrecht, pp 321–340, 669 pp

Vincent WF, Neale PJ (2000) Mechanisms of UV damage to aquatic organisms. In: de Mora S, Demers S, Vernet M (eds) The effects of UV radiation in the marine environment. Cambridge University Press, Cambridge, pp 149–176

Vincent WF, Roy S (1993) Solar ultraviolet–B radiation and aquatic primary production: damage, protection, and recovery. Environ Rev 1:1–12

Vincent WF, Downes MT, Castenholz RW, Howard-Williams C (1993) Community structure and pigment organisation of cyanobacteria-dominated microbial mats in Antarctica. Eur J Phycol 28:213–221

Vincent WF, Mueller DR, Van Hove P, Howard-Williams C (2004) Glacial periods on early Earth and implications for the evolution of life. In: Seckbach J (ed) Origins: genesis, evolution and diversity of life. Kluwer Academic Publishers, Dordrecht, pp 481–501

Vinebrooke RD, Leavitt PR (1996) Effects of ultraviolet radiation on periphyton in an alpine lake. Limnol Oceanogr 41:1035–1040

Walker JJ, Pace NR (2007) Phylogenetic composition of Rocky Mountain endolithic microbial ecosystems. Appl Environ Microbiol 73:3497–3504

Walsby AE (1994) Gas vesicles. Microbiol Rev 58:94–144

Ward DM, Castenholz RW (2000) Cyanobacteria in geothermal habitats. In: Whitton BA, Potts M (eds) Ecology of cyanobacteria: their diversity in time and space. Kluwer Academic Publishers, Dordrecht, pp 7–59, 669 pp

Weisse T (1993) Dynamics of autotrophic picoplankton in marine and freshwater ecosystems. Adv Microb Ecol 13:327–370

Whitehead RF, de Mora SJ, Demers S (2000) Enhanced UV radiation – a new problem for the marine environment. In: de Mora S, Demers S, Vernet M (eds) The effects of UV radiation in the marine environment. Cambridge University Press, Cambridge, pp 1–34

Willis KJ, Bennett KD, Birks HJB (2009) Variability in thermal and UV-B energy fluxes through time and their influence on plant diversity and speciation. J Biogeogr 36:1630–1644

Wingard CE, Schiller JR, Castenholz RW (1997) Evidence regarding the possible role of c-phycoerythrin in ultraviolet-B tolerance in a thermophilic cyanobacterium. Photochem Photobiol 65:833–842

Wu H, Gao K, Villafañe VE, Watanabe T, Helbling EW (2005) Effects of solar UV radiation on morphology and photosynthesis of filamentous cyanobacterium *Arthrospira platensis*. Appl Environ Microbiol 71:5004–5013

Xing P, Hahn MW, Wu QL (2009) Low taxon richness of bacterioplankton in high-altitude lakes of the eastern Tibetan Plateau with a predominance of *Bacteroidetes* and *Synechococcus* spp. Appl Environ Microbiol 75:7017–7025

Zalar A, Tepfer D, Hoffmann SV, Kenney JM, Leach S (2007a) Directed exospermia: I. biological modes of resistance to UV light are implied through absorption spectroscopy of DNA and potential UV screens. Int J Astrobiol 6:229–240

Zalar A, Tepfer D, Hoffmann SV, Kollmann A, Leach S (2007b) Directed exospermia: II. VUV-UV spectroscopy of specialized UV screens, including plant flavonoids, suggests using metabolic engineering to improve survival in space. Int J Astrobiol 7:1–11