

The role of solar UV radiation in the ecology of alpine lakes

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Abstract

Solar ultraviolet radiation (UVR, 290–400 nm) is a crucial environmental factor in alpine lakes because of the natural increase of the UVR flux with elevation and the high water transparency of these ecosystems. The ecological importance of UVR, however, has only recently been recognized. This review, examines the general features of alpine lakes regarding UVR, summarizes what is known about the role of solar UVR in the ecology of alpine lakes, and identifies future research directions. Unlike the pattern observed in most lowland lakes, variability of UV attenuation in alpine lakes is poorly explained by differences in dissolved organic carbon (DOC) concentrations, and depends mainly on optical characteristics (absorption) of the chromophoric dissolved organic matter (CDOM). Within the water column of lakes with low DOC concentrations (0.2–0.4 mg l⁻¹), UV attenuation is influenced by phytoplankton whose development at depth (i.e. the deep chlorophyll maximum) causes important changes in UV attenuation. Alpine aquatic organisms have developed a number of strategies to minimize UV damage. The widespread synthesis or bioaccumulation of different compounds that directly or indirectly absorb UV energy is one such strategy. Although most benthic and planktonic primary producers and crustacean zooplankton are well adapted to high intensities of solar radiation, heterotrophic protists, bacteria, and viruses seem to be particularly sensitive to UVR. Understanding the overall impact of UVR on alpine lakes would need to consider synergistic and antagonistic processes resulting from the pronounced climatic warming, which have the potential to modify the UV underwater climate and consequently the stress on aquatic organisms. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

In this review, I will examine the general features of alpine lakes regarding solar UV radiation (UVR, 290–400 nm), summarize the work done on its role in the ecology of these ecosystems, and identify topics for future research. Most of the examples will refer to research done in the Alps, but specific references to other mountain areas will also be made.

Alpine or high mountain lakes are defined as lentic ecosystems located above the treeline. The treeline, however, depends more on temperature than on altitude [1] and therefore on the latitude. So, while the alpine zone at Mount Kenya (0° N) is between ~3500 and 4500 m above sea level (a.s.l.), it is between ~2000 and 3000 m a.s.l. in the Alps (45° N), and around 1000–2000 m a.s.l. at Mount Denali, Alaska (63° N) [2]. The definition of alpine lakes

is based on a zonation scheme developed by botanists [3]. However this definition is not arbitrary because the relative position of the lakes with respect to the treeline imparts important chemo-optical characteristics to the water as discussed below.

Alpine lakes in the Alps originated after the last glacial retreat ~10,000 years ago [4]. Because they are remote and difficult to access, there is generally no direct human influence in their catchments. This condition does not necessarily imply that these ecosystems are pristine because many pollutants are introduced through regional and long-range atmospheric transport (see Section 6). Most of the lakes in the Alps are small (area <5 ha) and generally shallow ($Z_{\max} < 15$ m) and, depending on their altitude, they are ice- and snow-covered for up to 3/4 of the year. These ecosystems can be considered as harsh environments because organisms have to cope with low nutrient conditions/low food availability, low temperature, short growing seasons (3–5 months), low pH (e.g. in crystalline regions), extreme changes in light conditions between the

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ice-covered and ice-free situations, and periods of strong solar UVR.

Alpine lakes receive generally higher incident solar UV fluxes than low-elevation lakes due to the natural increase of UVR flux with elevation. This is most evident for the shortest wavelengths of the UV-B range (290–320 nm). Measurements of UVR in the Alps between 577 and 3576 m a.s.l. with a Robertson–Berger sunburn-meter have indicated an annual average UV-B increase of ~19% per 1000 m [5]. This value, however, is different for other mountainous regions due to differences in air humidity, pollution levels, elevation range, as well as in the instrumentation used [5–7]. For example, measurements with a spectrophotometer done between 1980 and 2965 m a.s.l. in the German Alps, yielded a UV-B increase of only 5 to 10% per 1000 m [7]. Although the thickness of the cloud layer has been reported to decrease with elevation [8], little information is available on cloud cover at different elevations to evaluate whether the time-integrated incident UVR, particularly during the ice-free period, also increases.

An important change that takes place above the treeline is the reduction of dissolved organic matter (DOM) concentration in lakes. For example, a survey of 57 lakes in the Alps revealed that the mean concentration of DOC, an indicator of the concentration of DOM, decreases by 64% from 2000 to 2800 m a.s.l. [9]. Similar observations have been made in the Cascade Mountains, USA, across an elevation range of 600 to >2000 m a.s.l. [10]. This pattern reflects the decrease in allochthonous DOC yield arising as a result of reduced soil development and terrestrial vegetation cover with increasing elevation in such catchments. Concomitant with reduced DOM concentrations, there is a significant qualitative change in DOM composition (e.g. lower aromaticity), which is reflected in the optical properties of this material like, e.g. its low DOC-specific absorption and low fluorescence, and that suggests a higher contribution of CDOM from algal origin [11–13]. Such observations are crucial to understanding the high UV transparency of alpine lakes.

2. Overview of UV research in alpine lakes

In the earlier research on alpine lakes, solar UVR was rarely identified as an important environmental variable. However some publications, mostly written in German or Italian (and generally not cited) are worth mentioning as antecedents or to understand why UVR was not considered of interest at the time.

Brehm [14] was among the first authors to refer to the importance of UVR for alpine aquatic organisms. This author suggested that carotenoids were responsible for the red appearance in zooplankton and other organisms like the 'snow algae' *Chlamydomonas nivalis*, and that these pigments had a photo-protective role.

In the 1940s, Merker [15] discussed the importance of dissolved organic substances for UV attenuation in freshwaters. His pioneer measurements of UV absorption and fluorescence (excitation with UV radiation at 366 nm) of the dissolved fraction (filter type not specified) in oligotrophic pre-alpine lakes and productive ponds, led him to conclude that dissolved organic substances reduce the penetration of UV and that this is largely affected by lake productivity. Merker also described temporal changes in fluorescence of filtered water and concluded that the lower values in winter are related to the low in-lake production and export of organic matter from the catchment. Finally, Merker [15] remarked that *Daphnia pulex* and amphibians were highly sensitive to the UV portion of solar radiation.

During the 1960s, discussions about the role of UVR were mainly centered on the effects on phytoplankton and primary production. Rodhe [16] and Rodhe et al. [17], investigating possible causes for the characteristic deep chlorophyll maximum (DCM) observed in alpine lakes, suggested that UVR could be responsible for this distribution pattern of phytoplankton. Based on measurements of UV penetration (UG1 filter, 300–400 nm) in Lapland lakes, which showed high penetration (a 10% depth of up to 28 m), and on published results about UV inhibition of photosynthesis in the sea, Rodhe et al. [17] argued that UVR in alpine lakes not only depresses phytoplankton production, but also penetrates deeply into the water column (because of the scarcity of phytoplankton and other light-absorbing matter). In contrast, Findenegg [18] concluded, after evaluating a series of experiments with cultures (*Chlorella* sp.) and natural phytoplankton populations exposed to solar radiation in quartz and glass bottles for 2 h at different depths, that the effect of UVR on phytoplankton in oligotrophic lakes is minimal and restricted only to the upper first meter of the water column. However the lakes, where the experiments were done, although oligotrophic, had relatively low transparency to UVR. Despite this, he found clear evidence for UV photoinhibition of phytoplankton production in some of the lakes. Nevertheless, Findenegg argued against the hypothesis of UVR as cause for the inhibition of primary production in oligotrophic lakes (cf. [17]). Furthermore, though Findenegg acknowledged that in certain lakes the transmission of UVR was considerable, he concluded that UV-B radiation (wavelengths below 315 nm) was not present in the solar spectrum and consequently could not be present underwater.

Pechlaner [3], in his 1970s review of the factors controlling phytoplankton production in alpine lakes, again refuted Rodhe et al.'s [17] hypothesis. Pechlaner [3] was strongly influenced by Haldall's arguments [19] on the modest ecological importance of UVR and by the statement that near UVR (i.e. 310–390 nm) caused the same effects on biological material as visible light did on a quantum basis. Probably, Pechlaner's view explains the lack of interest of UV studies in large research projects that

included alpine lakes during the 1970s and 1980s, like the International Biological Program.

3. UV transparency and attenuation

Alpine lakes, with the exception of those fed by turbid glacier streams, are among the most UV transparent aquatic systems in the world. In a study of 26 lakes in the Alps and Pyrenees, the diffuse attenuation coefficient (K_d) at the nominal wavelength of 320 nm (filter radiometer PUV-500, Biospherical Instrument, CA) ranged from 0.17 to 2.5 m^{-1} with an average of 0.55 m^{-1} for lakes with catchments dominated by bare rocks [12]. The lowest K_d value in that dataset was similar to those found in ice-covered Antarctic lakes of the Dry Valley (0.05–0.12 m^{-1}) with low DOC content [20], or other alpine lakes like Laguna Negra, Chile (0.16–0.29 m^{-1}) [21,22] and Schmall, Argentina (0.17 m^{-1}) [23].

As discussed in Section 1, the optical characteristics of DOM are key to the explanation of why high UVR transparency is characteristic of alpine lakes. Unlike lowland lakes, where the concentration of DOC is a good predictor of UV transparency, the variability in UV transparency among alpine lakes (e.g. K_d at 320 nm) is better explained by the absorption of DOM (94%) than by the concentration of DOC (59%) or DOM fluorescence (72%) [12]. Therefore, the use of DOC concentrations to infer present or past values of UV transparency in lakes situated above treeline should be done with caution.

In alpine lakes of low DOC concentrations, phytoplankton contribute significantly to the UV attenuation in the water column [12,24]. For example, in Gossenköllesee, Austria (DOC: $\sim 0.3 \text{ mg l}^{-1}$), the development of the DCM after ice-break causes a 43% increase in UV attenuation (nominal wavelength of 340 nm) in only 2 weeks [24]. The magnitude of UV attenuation, is, however, not equivalent at all wavelengths being higher at 320 and 340 nm than at 305 nm [24]. This pattern has been associated with the occurrence of the UV-absorbing compounds (see Section 4) in plankton known as mycosporine-like amino acids [24,25].

Photobleaching of DOM is another potential factor causing temporal changes in UV transparency in alpine lakes. The lower values in DOC-specific absorptivity generally found in surface waters compared to deeper layers suggest the importance of photobleaching in these lakes [12].

4. Minimizing UV damage in aquatic organisms

Organisms living in alpine lakes have developed, among other strategies to minimize damage when exposed to solar UVR, the synthesis of compounds that directly or indirectly absorb UV energy, like melanin, carotenoids,

scytonemin, and mycosporine-like amino acids (MAAs). For example melanization of the dorsal portion of the carapace and the antennae is typically observed in *Daphnia spp.* from alpine, and high-latitude lakes [26,27].

Carotenoids that do not directly absorb UVR, but are effective quenchers of radical oxygen species, are found in phototrophic and heterotrophic organisms in alpine lakes. A notable example of high accumulation of protective secondary carotenoids, particularly astaxanthin and its esters, is found in cysts of the green algae *Chlamydomonas nivalis* [28]. Copepods from alpine lakes can also accumulate high amounts of carotenoids that give them the intense red appearance typical for alpine forms [14,26,29,30]. The concentration of these compounds in calanoid copepods has been found to increase with lake elevation and shallowness of the systems [31].

A remarkable UV protecting compound is scytonemin, a yellow–brown pigment only found in the sheaths of cyanobacteria, especially those living under conditions of intense solar radiation [32]. Scytonemin has a maximum in vivo absorption at 370 nm in the UV-A range (320–400 nm), and similar compounds accumulated in the sediments have been used to reconstruct past changes of UVR light climate in alpine lakes [33].

The last class of UV-absorbing compounds are the mycosporine-like amino acids (MAAs), a family of water-soluble, low-molecular weight, compounds with high molar extinction coefficients, and absorption maxima between 309 and 360 nm. These compounds have been found in different taxa of marine organisms ranging from bacteria to fish [34–36] and more recently in phytoplankton, benthic cyanobacteria, and in the copepod *Cyclops abyssorum taticus* from a transparent alpine lake [24,25].

Information on both the efficiency of MAAs in protecting alpine aquatic organisms and the factors controlling their synthesis (e.g. light intensity, UV wavelengths, nutrients) is still lacking. The high concentration found, for example, in epilithic cyanobacteria or algal mats [25,37], or the decrease of MAA concentrations in phytoplankton with depth [25], suggest that they are important for UV protection in organisms exposed to high UV fluxes. Other organisms like *C. abyssorum taticus*, strongly bioaccumulate MAAs and may attain concentrations of up to 2.3% of the dry weight or even higher [25,38]. Bioaccumulation of MAAs has also been reported for populations of the copepod *Boeckella titicacae* from the tropical high altitude Lake Titicaca [39] and for populations of *B. gracilipes* from Laguna Negra, Chile [30].

The concentration of MAAs in populations of *C. abyssorum* and *C. abyssorum taticus* from lakes in the Alps has been found to increase exponentially with lake elevation and underwater UV transparency [38]. Although late development stages of this species show daily vertical migration and stay at the deepest part of the lake during daytime [30], in shallow transparent lakes they will not

find enough depth refuge from UVR. They need, therefore, protective substances such as MAAs, which are predicted to become more important as K_{d-UVR} decreases. In fact, the physical refuge of the lakes, estimated as the ratio of the depth at which surface UV-B radiation is attenuated to 1% to the maximum depth, resulted in the best predictor (86% variability explained) of MAA concentrations in these copepod populations [38].

5. UV effects on aquatic organisms

Alpine lakes are naturally fishless, however, there is good historical evidence that man has been introducing fish to such systems since ca. 1500 A.D. [4]. Detrimental effects of solar UV radiation (sunburn) on fish are known for farmed species like rainbow trout, *Salmo gairdneri*, kept at high elevations like in Lake Titicaca (3810 m a.s.l.) [40]. A significant reduction in the number of mucus secreting (globet) cells has also been observed in the dorsal epidermis of natural populations of minnow *Phoxinus phoxinus* (fry) in the littoral zone of Lichtsee (2104 m a.s.l.), Austria [41].

The community structure of zooplankton in alpine lakes is relatively simple, with few dominant species [42]. Thus, for example, *Cyclops abyssorum taticus* and *Arctodiaptomus alpinus* are the dominant copepod species found in alpine lakes of the Austrian Alps, while *Daphnia* spp. are absent in many lakes probably due to the introduction of Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*).

Studies on the survival of red pigmented copepods *C. abyssorum taticus* (Alps) and *Boeckella gracilipes* (Andes) have shown that these species are very resistant to ambient levels of solar UVR, even when exposed under extreme conditions, i.e. for 3 days close to the surface [30]. Long-term experiments (48 days) using enclosures have also confirmed the low sensitivity of *B. gracilipes* [21]. In contrast, in the same experiment, the littoral cladoceran *Chydorus sphaericus* and the rotifer *Lepadella ovalis* from Laguna Negra (2700 m a.s.l.), Chile, were very sensitive to UV-B radiation [21]. Similar results, i.e. no sensitivity of pigmented calanoid copepods (*Hesperodiaptomus arcticus*), but of unpigmented rotifer species like *Keratella quadrata* have been observed in a long-term enclosure (30 days) experiment done at Pipit Lake (2217 m a.s.l.), Canada [43].

Phytoplankton populations in high-mountain lakes of the Alps are dominated by nanoplanktonic (2–20 μm diameter) and motile species of chrysophytes, dinoflagellates and cryptophytes [9,17,44,45]. Only in 13% of 48 lakes in the Alps, diatoms (Bacillariophyceae) represented more than 50% of the total biovolume. Other groups like Euglenophyceae, Xanthophyceae and Cyanophyceae are numerically of minor importance [9,44,45]. Results from short-term experiments with natural or simulated solar

radiation have shown that UVR (mainly UV-A) causes significant inhibition of phytoplankton photosynthesis in the upper first metres of the water column in alpine lakes or systems located at high elevations like Lake Titicaca [22,39,46]. In contrast, results from a long-term enclosure experiment (16 days) in a transparent lake from the Alps indicated no UV-B effects on phytoplankton growth rate and changes in species composition [47]. However, the growth of some species, e.g. the dinoflagellates *Gymnodinium cnecoides* and *G. uberrimum*, was negatively affected by UV-A plus photosynthetically active radiation (PAR, 400–700 nm). Nevertheless, the sensitivity of these species was consistent with their diurnal vertical distribution in the lake; they occupy the deepest water layers during daytime. Lack of long-term UV effects (30 days) on phytoplankton assemblages consisting mainly of picocyanobacteria, chrysophytes, cryptophytes, and dinoflagellates has also been observed in Pipit Lake, Canada [43]. In a long-term enclosure experiment in Laguna Negra, Chile, growth of *Ankyra judayi* (Chlorophyta) was unaffected by the presence of UV-B, while the diatoms *Fragilaria construens* and *F. crotonensis* were dominant in the treatment without UV-B radiation [21].

Another important component among primary producers of alpine lakes is the community attached to substrates (epilithon and epipelon). Long-term experiments to assess the impact of UVR on benthic algae in Pipit Lake, Canada, have shown that the standing crop of the epilithic microalgae in the littoral zone, particularly diatoms, is strongly suppressed by UV-B radiation [43]. In contrast, the standing crop of the epipellic algal community remains unaffected by UVR [43]. Furthermore, results from colonization experiments of artificial substrates in Snowflake Lake (2320 m a.s.l.), Canada, have demonstrated the existence of a species-specific UV sensitivity among diatoms [48]. In particular, among seven periphytic diatom species, the growth of *Achnanthes minutissima* was strongly suppressed by ambient levels of UVR [48]. Although UVR plays a major role in shaping the structure of epilithic algae [48], natural epilithic communities of transparent alpine lakes are dominated by cyanobacteria [48,49].

Heterotrophic bacteria seem to be very sensitive to solar UVR. Short-term experiments (3–4 h) have shown that bacterial activity (incorporation of [^3H]thymidine and [^{14}C]leucine) can be reduced by solar radiation close to the water surface by up to ~70% [50]. The incorporation rate was inhibited by UV-A radiation and PAR; these wavebands contributing almost equally to the inhibition [50]. However, long-term experiments (16 days) made in Gossenköllesee (2417 m a.s.l.), Austria, under in situ conditions using enclosures of 1 m³, have shown that the growth of non-filamentous bacteria (<10 μm long) and the cell-specific activity ([^3H]thymidine incorporation), were negatively affected by UV-B radiation [51].

In contrast to the effect observed for the assemblage of

small heterotrophic bacteria, filamentous bacteria (>10 μm long) that represent only <4% of the total abundance, but up to ~70% of the total bacterial biovolume in Gossenköllesee, were not affected by UV-B radiation, indicating that, like for many other members of the plankton, important differences among groups or species in UV sensitivity exist [51].

Another component of the microbial food-web sensitive to UVR are the heterotrophic flagellates. During the same long-term experiment in Gossenköllesee described above, growth of heterotrophic flagellates and the rate of bacterial consumption were reduced by UV-B radiation [51]. In a recent study in Gossenköllesee, the impact of UVR on bacterivory, however, was found to be mainly restricted to the upper 2.5 m and, when integrated for the whole water column, the loss was <25% [52].

Information on the UV sensitivity of ciliates from alpine lakes is only available for *Urotricha pelagica* and *U. furcata*. These species are relatively resistant to solar UV-B radiation and only a small reduction in their net growth rate has been observed during the first week of a long-term experiment [51].

Viruses are numerically the most abundant biological agents in aquatic ecosystems. For example, in the only two available studies for alpine lakes, the abundance of planktonic viruses ranged from 10^5 to 10^7 ml^{-1} [53,54]. Solar UVR can affect the infectivity as well as the integrity of viruses. Experimental evidence suggesting that viral integrity and/or production are impaired by UV-B radiation has been found during an enclosure experiment in Gossenköllesee, Austria [51]. In addition, during the ice-free season in the same lake, the abundance of viruses in the upper 2 m of the water column has been found to be negatively correlated with the integral of global solar radiation received 3 days before sampling [54], suggesting that UVR plays an important role in the dynamics of this planktonic group.

6. Pollutants and solar UV radiation

Alpine lakes, though remote, are not always pristine environments as demonstrated by recent studies that report high concentrations of pollutants like polycyclic aromatic hydrocarbons (PAHs), organochlorine compounds, and heavy metals in snow, water, sediments, and fish [55–58]. These pollutants result from regional and long-range atmospheric transport, and in some cases like in some organochlorines, their concentration can be enriched due to cold-condensation of volatile compounds [57]. The presence of these pollutants alone may exert a negative impact on the biota of these ecosystems; however, the interaction with solar UVR can trigger a series of photochemical reactions that could reduce their concentration, e.g. methylmercury (photodemethylation and photoreduction/volatilization) [59], or enhance their toxicity, e.g. PAHs

[60]. The photoinduced toxicity of PAHs has not yet been studied in organisms from alpine lakes, but two characteristics of these systems, namely the low water temperature (i.e. low excretion rates), and low concentration of humic substances, known to reduce the photoinduced toxicity of PAHs [61], suggest that UVR may have a crucial role for the toxicity of these compounds in many alpine lakes.

7. Synergistic and antagonistic effects of climatic warming on UV stress

The ecosystem response of alpine lakes, as well as of other freshwater ecosystems, to present and increased levels of solar UV-B radiation remains poorly understood. This results first from the problem of the physical scale considered in most field studies, which assesses the responses of only some of the compartments of the ecosystem, and second from the large variability in sensitivity to UVR observed among individuals, populations, and species. Nevertheless, although the trend for UV-B radiation increase at mid-latitudes is low [62], the assessment of the response of alpine lakes to UV-B radiation cannot be isolated from other important environmental changes that take place in several regions of the Earth (e.g. climatic warming). Climatic warming, for example, has been particularly pronounced in the Alps, with a mean air temperature increase of 1°C since 1985 [63].

In assessing different scenarios it is important to differentiate among potential responses of the ecosystem in relation to the time scale at which climate warming is acting. On a short-time scale, one of the most apparent effects of climate warming is a decrease in the snow- and ice-cover duration. The disappearance of the winter cover produces a dramatic change in the underwater UVR climate. For example, at similar solar zenith angles, UV irradiance levels during the ice-free period are one order of magnitude higher than under 1.8 m thick ice- and snow-cover [52]. This change may exacerbate the UV impact if it occurs before the summer solstice (i.e. highest UV flux) as observed in years with warm springs. In addition, earlier disappearance of the winter cover may result in a stronger temperature stratification, which eventually could lead to trapping of non-motile organisms close to the surface. Overall, these processes will increase the stress of UVR on the ecosystem.

On a longer time scale, the increase in mean air temperature could favor the development of terrestrial vegetation in the catchment, that may result in an increase of chromophoric DOM-export to the lakes near the treeline [9,64]. Although there is sparse information on DOC-export rates to alpine lakes, this scenario is supported by the finding that the alpine-nival flora in some mountainous regions like in the western Austrian and eastern Swiss Alps has moved upward in recent years [65]. Considering that

drought periods have not been associated with climatic warming in the Alps [63], a potential increase in CDOM export to the lakes will likely reduce UV transparency and consequently the UV stress on these ecosystems.

8. Conclusions

Although some interesting papers on the role of UVR in alpine environments were published in the 1940s, the importance of UVR as a crucial environmental factor in alpine lakes has only recently been recognized. Most alpine lakes are highly transparent to UVR and the variability in attenuation among lakes can be explained by the absorption of DOM. In many alpine lakes, however, particularly in those having low DOC concentrations, phytoplankton substantially contributes to the UV attenuation in the water column, and consequently, changes in its abundance, for instance the formation of the DCM, cause important temporal changes in UV transparency.

Organisms living in alpine lakes have evolved several strategies to cope with UVR including the synthesis of UV-absorbing compounds. Until recently, some of them, like MAAs, were known only for marine organisms. Studies on the sensitivity of organisms and biological processes to solar UV radiation in alpine lakes are still scarce, probably because of the difficulty to perform *in situ* experiments in these systems. Most information about the impact of UV radiation in alpine organisms is at the community and, in some groups, at the species level. Results from these experiments have shown that the impact of present levels of UV-B radiation on natural planktonic and benthic communities is low to moderate. However, viruses, heterotrophic flagellates, and bacteria appear to be particularly sensitive to solar UVR, which may have important consequences for the C-cycling in alpine lakes. The results from these studies also indicate the importance of choosing different time scales to assess the impact of UVR on biological processes, and of measuring the impact on several cell targets that may have different sensitivity to UV-B and UV-A radiation. Still there is little information to conclude whether the effects of solar UVR are mainly exerted directly or indirectly, *i.e.* mediated through the food-web. Finally, the potential impact of UVR on these ecosystems needs to be assessed considering synergistic and antagonistic processes, which are expected to result from the pronounced climatic warming and the interaction with pollutants supplied by long-range atmospheric transport.

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