

Effects of UV radiation on aquatic ecosystems and interactions with climate change

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The health of freshwater and marine ecosystems is critical to life on Earth. The impact of solar UV-B radiation is one potential stress factor that can have a negative impact on the health of certain species within these ecosystems. Although there is a paucity of data and information regarding the effect of UV-B radiation on total ecosystem structure and function, several recent studies have addressed the effects on various species within each trophic level. Climate change, acid deposition, and changes in other anthropogenic stressors such as pollutants alter UV exposure levels in inland and coastal marine waters. These factors potentially have important consequences for a variety of aquatic organisms including waterborne human pathogens. Recent results have demonstrated the negative impacts of exposure to UV-B radiation on primary producers, including effects on cyanobacteria, phytoplankton, macroalgae and aquatic plants. UV-B radiation is an environmental stressor for many aquatic consumers, including zooplankton, crustaceans, amphibians, fish, and corals. Many aquatic producers and consumers rely on avoidance strategies, repair mechanisms and the synthesis of UV-absorbing substances for protection. However, there has been relatively little information generated regarding the impact of solar UV-B radiation on species composition within natural ecosystems or on the interaction of organisms between trophic levels within those ecosystems. There remains the question as to whether a decrease in population size of the more sensitive primary producers would be compensated for by an increase in the population size of more tolerant species, and therefore whether there would be a net negative impact on the absorption of atmospheric carbon dioxide by these ecosystems. Another question is whether there would be a significant impact on the quantity and quality of nutrients cycling through the food web, including the generation of food proteins for humans. Interactive effects of UV radiation with changes in other stressors, including climate change and pollutants, are likely to be particularly important.

Introduction

The important scientific results on the effects of solar UV radiation published during the past four years are assessed for aquatic ecosystems. In total, aquatic ecosystems (1) absorb a similar amount of atmospheric carbon dioxide as terrestrial ecosystems, (2) produce half of the biomass on our planet,¹ (3) are a major source for human food supply and drinking water, and (4) are economically important for pharmaceutical and chemical industries.^{2–11} Solar UV radiation can damage aquatic organisms and decrease the productivity of aquatic ecosystems. These

effects of UV radiation may reduce the photosynthetic uptake of atmospheric carbon dioxide and affect species diversity, ecosystem stability, trophic interactions, and global biogeochemical cycles. The negative effects of UV radiation may be augmented by other environmental changes,^{12,13} including global climate change¹⁴ and pollution that result in vast “dead zones”,¹⁵ which collectively turn “estuaries and even parts of the oceans into barren wastelands”.¹⁶ Many bacteria, plants and animals cope with UV stress with adaptive responses.^{17–20}

We briefly assess current knowledge on factors controlling the penetration of solar UV radiation into the water column, as well as protective mechanisms of aquatic organisms against solar UV radiation (Fig. 1). This is followed by a more in-depth assessment of the impacts of UV radiation on different components of aquatic ecosystems, including bacteria, cyanobacteria, phytoplankton, seaweeds (macroalgae), and consumers (zooplankton, amphibians, fish, corals and other animals). The interactive effects of UV radiation with pollutants and changing oceanic pH are also discussed.

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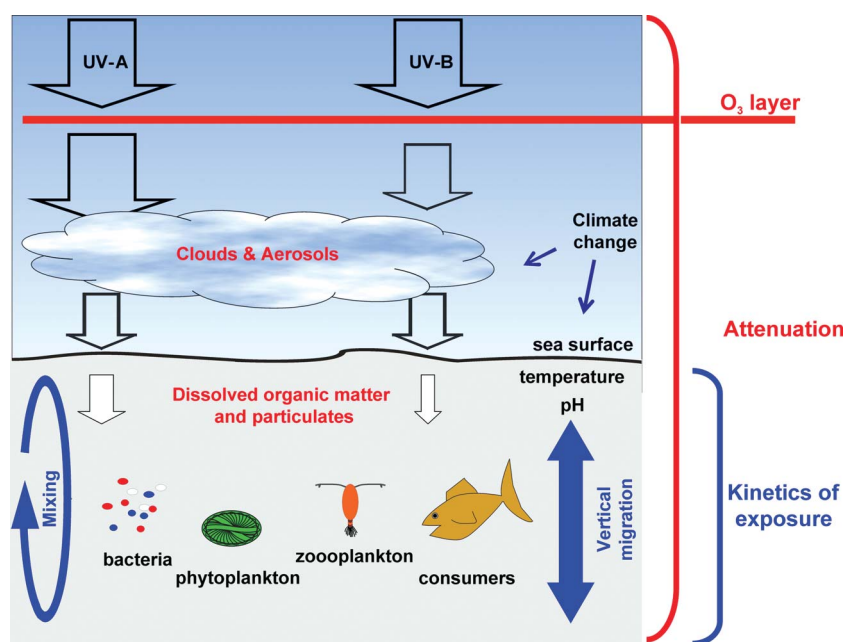


Fig. 1 Main factors affecting the quantity and quality of UV radiation received by aquatic organisms. Modified from Gonçalves *et al.*²⁹³

UV radiation in the water column and climate change effects

Transmission into natural waters

The transmission of solar UV radiation into the water column depends on variables in the atmosphere and in the water that affect the amount of UV radiation and wavelength distribution.^{21,22} Water transparency to UV depends on the optical properties of the water itself,²³ dissolved material, phytoplankton concentration, and the density of suspended particles.^{24,25} Coloured dissolved organic matter (CDOM) is a major factor controlling optical characteristics of freshwater and coastal habitats, thus reducing UV exposures of organisms in the water. It is generated through microbial degradation of organic material from macroalgae and plankton as well as terrestrial plants.^{26,27} Quality and quantity of CDOM thus vary seasonally due to variations in these aquatic processes and rainfall events.^{28,29} CDOM plays direct and indirect roles in biogeochemical cycles.³⁰

Some of the most UV-transparent waters are systems with extremely low CDOM concentrations such as the hyper-oligotrophic waters of the South Pacific Gyre where diffuse attenuation coefficients indicate that 1% of incident surface UV radiation (at 325 nm) reaches as deep as 84 m.³¹ In some of the clearest lakes 1% of UV (at 320 nm) penetrates as deep as 27 m (Lake Tahoe, California–Nevada, USA),³² or 62 m (Crater Lake, Oregon, USA).³³ Due to their high elevation and location above the treeline, alpine lakes have very little CDOM and also higher levels of incident UV, giving them some of the highest overall UV exposure levels in the world, with important implications for species composition (Fig. 2).³²

Solar UV radiation causes photodegradation of CDOM,^{34–36} this being a key process in the carbon cycle.^{37,38} The breakdown of larger molecules into smaller fragments stimulates bacterial activity and can alter the species composition of bacterioplankton,³⁹

while degradation of organic matter from several aquatic plants releases nutrients such as phosphorus and iron.^{40–42} The photodegradation of CDOM increases transmission of solar UV radiation in the water column, potentially enhancing deleterious effects on aquatic organisms.³⁶ In freshwater lakes, measurements of CDOM absorption can be used as a proxy for UV transmission and prediction of water quality, as was done in the shallow Lake Taihu, China, an important drinking water resource.⁴³ In Lake Tahoe in California–Nevada, strong inshore-offshore gradients and seasonal changes in transparency to UV-A (380 nm) radiation provide a more sensitive indicator of environmental change than variations in visible light transparency.³² Water samples taken at different locations in the Bering Sea and exposed to solar UV radiation at controlled temperatures showed an 18–55% decrease in CDOM at some stations.⁴⁴ At other stations, up to a 16-fold increase in CDOM absorption was observed and attributed to decreases in the ability of microbes to degrade CDOM derived from algal blooms. Experiments with freshwater samples from Antarctica and North America have shown that UV-induced production of singlet oxygen by CDOM contributes to degradation of dissolved free amino acids.⁴⁵

Climate change and UV radiation in the water column

Climate change and other stressors have important effects on the underwater UV radiation through a variety of mechanisms including changes in UV transparency and mixing depth of the surface waters. The consequent changes in UV exposure have important implications for processes ranging from UV inactivation of water-borne human pathogens to carbon cycling. Some of the major consequences of climate-change effects on aquatic ecosystems are changing temperature, precipitation and ice melting. In some regions warmer air temperatures and reduced precipitation are predicted by climate models, while in other

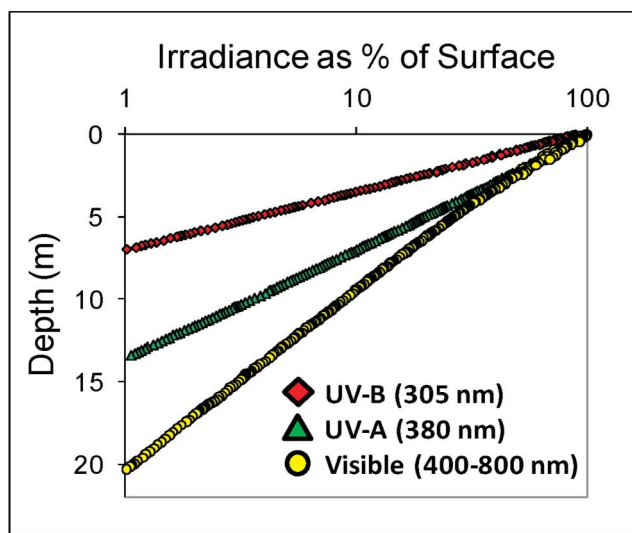
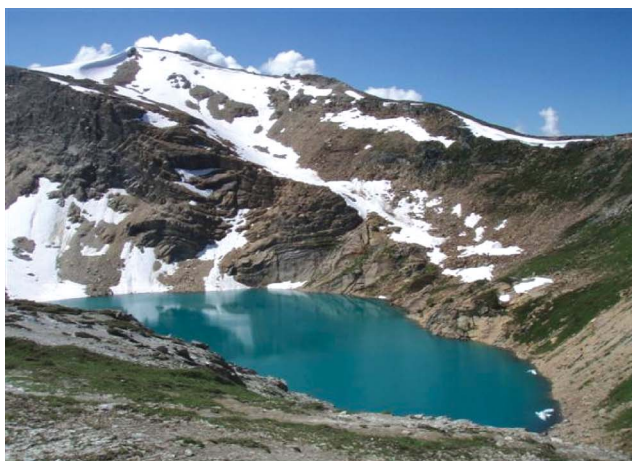


Fig. 2 Profiles of UV-B, UV-A radiation, and visible light penetration in Sunlite Lake, an alpine lake in the Canadian Rocky Mountains. The high elevation of alpine lakes leads to high incident UV radiation, while the low levels of DOM in alpine lakes lead to high UV transparency of the waters. The result is that aquatic organisms are exposed to higher levels of damaging UV radiation in alpine lakes than in any other aquatic ecosystem on Earth.

regions the opposite is expected.⁴⁶ Both of these will affect the depth of the surface mixed layer.⁴⁷ Shallower surface mixing depths have the potential to increase UV exposure of aquatic organisms that live in the upper layers.

Over the past two decades, concentrations of DOM have doubled in inland waters across major portions of north-eastern North America and Europe.^{48–50} The reasons for this appear to be related largely to reductions in acid deposition,^{49,50} but climate may also play an important role.^{51,52} One major concern is that increased DOM concentrations will reduce the natural levels of solar UV that are important for inactivating human pathogens such as *Cryptosporidium* (see ref. 53–55 and Norval *et al.*⁵⁶).

Optical properties in polar freshwater and marine systems are further modulated by snow and ice cover as well as by dissolved and particulate material from runoff during melting.⁵⁷ Climate-driven decreases in the duration of ice cover have been observed in polar marine waters.^{58–60} These conditions are predicted to undergo large changes due to climate change in the future. A model based

on several environmental factors, such as concentrations of DOM, weather conditions, and water acidification, indicated that the dominant effects of climate change on the organisms of the upper water layers of small lakes operate through processes that affect water transparency.^{61,62} The number of days above freezing is also an important predictor of concentration of DOM.⁵² Very limited information is available on the balance between the interactive effects of climate-driven changes in temperature, precipitation, and quality and quantity of DOM, information that is necessary to decipher the net effects of climate change on UV exposure in aquatic ecosystems.

Protective mechanisms of aquatic organisms against UV radiation

All photosynthetic aquatic organisms are restricted to the sunlit upper layers of the water column where they are simultaneously exposed to solar visible and ultraviolet radiation. But many of the consumers in aquatic habitats are also found in this zone and will face the same environmental stresses. In addition to the current elevated levels of solar UV-B radiation in some regions, several aspects of global climate change may increase the exposure and impose additional stresses on these organisms. During evolution, aquatic organisms have developed a variety of protective strategies against solar UV stress. Motile biomass producers and consumers avoid excessive radiation by vertical migration. Sessile (attached) organisms rely on selection of habitat to limit solar exposure. Effective DNA repair systems eliminate DNA lesions encountered during high solar UV irradiation. Different taxonomic groups have developed a number of photoprotective substances such as melanins, mycosporines, mycosporine-like amino acids (MAAs), scytonemin, carotenoids, phycobiliproteins and several other UV-absorbing compounds of yet unknown chemical structure.²

Protection by UV-absorbing mycosporine-like amino acids (MAAs)

MAAs are the most common UV-sunscreens in many marine and freshwater organisms.^{63–65} They are small (<400 Da), intracellular, water-soluble compounds.¹ They absorb in the UV-A and UV-B range (between 309 and 362 nm) and are characterized by high molar extinction coefficients, photostability and resistance to many abiotic environmental factors. These substances seem to have evolved in cyanobacteria and are also synthesized by many phytoplankton groups and seaweeds (macroalgae). They are also found in animals as a result of being taken up through their diets. Nonetheless, a recent study identified the genes encoding enzymes for MAA biosynthesis in the starlet sea anemone *Nematostella vectensis*, indicating that some animals may be capable of MAA synthesis or modification.⁶⁶ Another option to obtain UV protection is to host MAA-producing symbionts as found in the marine algal-bearing ciliate (*Maristentor dinoferus*) isolated from coral reefs.⁶⁷ Corals are other examples which obtain MAAs from their photosynthetic symbionts.⁶⁸ In most corals, concentrations of MAAs vary seasonally and there is a negative correlation between MAA concentration and depth.^{69,70}

While the precise mechanisms of MAA biosynthesis are still not completely understood, recently several groups clarified the early stages of biosynthesis and identified the genes involved in the pathway in cyanobacteria and green and red algae.^{71,72}

MAA synthesis requires the availability of sufficient nitrogen in the environment.⁷³ Therefore, environmental factors reducing the concentration of nitrogen in water will compromise the capability of the organisms to protect themselves against solar UV radiation. Recent research has continued to clarify the biochemical pathway and molecular structure of the important UV-absorbing pigments.^{74,75} In addition to their role as UV-absorbing pigments, MAAs have other physiological functions such as osmotic regulation and scavenging of reactive oxygen species (ROS), which can contribute to adaptation strategies.^{76,77}

Changing environmental conditions due to global climate change (such as osmotic stress, salt stress, temperature) affect the biosynthesis of MAAs in several groups of aquatic organisms.⁷⁸ Desiccation plays a key role in the economically important *Porphyra* (nori) in maintaining high concentrations of MAAs,⁷⁹ thus allowing this seaweed to compete in the intertidal zone exposed to high levels of UV radiation. In diatoms, in contrast to many other aquatic organisms, MAAs are largely bound to the silica cell wall.⁸⁰ Therefore MAAs are found in sediments and can be used as markers for previous MAA concentrations in marine organisms.

Protection by other UV-absorbing pigments

The UV-absorbing scytonemin is exclusively synthesized by cyanobacteria.⁸¹ It is a dimeric, lipid-soluble pigment deposited in the extracellular sheaths of the cells.⁸² Like MAAs, synthesis of scytonemin requires the availability of nitrogen.⁷³ Periodic desiccation augments its productivity.⁸³ In *Nostoc punctiforme*, the response of a specific region in the genome associated with scytonemin synthesis was found to be activated (up-regulated) by exposure to UV radiation.^{84,85} Other UV-absorbing/screening compounds in marine organisms include 3-hydroxykynurenine, sporopollenin, melanin and fluorescent pigments.⁸⁶

Effects of UV-B radiation on aquatic bacteria

Bacteria, being decomposers, occupy a key position in the microbial loop of aquatic ecosystems, breaking down and mineralizing organic matter of decaying plants and animals. They form a link to higher trophic levels and are the main users of DOM. Water transparency strongly depends on the density of bacterial populations, and simultaneously phototransformation of DOM influences species distribution and bacteria concentrations in both freshwater and marine waters.^{87,88} Passive screening pigments are not effective in bacteria, because of their small size, which would require the concentration of these screening compounds to be excessively high to provide sufficient absorption. Therefore many aquatic bacteria are severely damaged by solar UV-B radiation at the molecular, cellular and population levels. Surface samples of heterotrophic bacteria collected during the BIOSCOPE cruise in the South East Pacific documented highest inhibition rates in bacterial productivity at noon time corresponding to the highest levels of solar UV-B radiation.⁸⁹

Possible strategies to mitigate UV-B radiation damage include high rates of reproduction and effective repair mechanisms.^{90,91} Immunoassay techniques applied to bacterioplankton samples collected off the coast of Chile (36°S) during the austral spring showed damaged DNA evidenced by a high induction of cyclobu-

tane pyrimidine dimers (CPD) after exposure to surface solar radiation.^{92,93} Bacteria in surface water samples showed a more effective photorepair mechanism than subsurface assemblages. Residual, chronic DNA damage was detected at the end of the experiment, and thus CPDs accumulated with time.

Bacteria with the highest UV-B tolerances found to date are from remote, high-altitude Andean lakes between 4200 and 4600 m above sea level.^{94,95} Different species have different sensitivities with respect to UV radiation.^{96,97} For solar (UV-A and UV-B) radiation and actively growing cells, the Gram-positive *Microbacterium maritropicum* was three times more resistant than the Gram-negative *Vibrio natriegens*.⁹⁸ These results indicate that increased exposure to solar UV-B radiation may affect bacterial assemblages, which may have consequences for higher trophic levels in aquatic ecosystems. It may also affect population densities of human pathogenic bacteria (see Norval *et al.*⁵⁶).

Consequences for cyanobacteria of elevated solar UV radiation and global climate change

Photosynthetic cyanobacteria are ubiquitous in freshwater and marine habitats from polar regions to the equator (Fig. 3). They are major biomass producers in the oceans and wetlands and responsible for the conversion of atmospheric nitrogen into nitrate and other compounds used by phytoplankton. Cyanobacteria are believed to have been the first photosynthetic organisms to produce oxygen 2.5–2.7 billion years ago. The enrichment of photosynthetically produced oxygen in the atmosphere over millions of years ultimately led to the development of the ozone (O₃) layer in the stratosphere.¹² Obviously, early ancestors of modern cyanobacteria were well adapted to high levels of solar UV-B and even UV-C radiation (below 280 nm) before the development of the ozone layer⁹⁹ and this could explain why some specialized cyanobacteria are capable of surviving in extreme habitats characterized by very high levels of UV-B radiation today.^{100,101}

In contrast, current solar UV-B radiation inhibits photosynthetic activity in most cyanobacteria.⁶⁴ One main target in photosynthesis is the D1 protein in the photosynthetic electron transport chain within the reaction centre of photosystem II.¹⁰² The damaged D1 proteins are replaced by newly synthesized molecules.¹⁰³ Furthermore, the phycobilin antenna pigments, responsible for collecting solar energy, are dismantled.¹⁰⁴

Solar UV radiation also modifies the morphological structure of filamentous cyanobacteria (*Arthrospira*) which is interpreted as a protection against solar radiation.^{105,106} This morphological alteration is prevented at elevated temperatures.^{107,108} In *Anabaena*, solar UV radiation also inhibited the development of heterocysts, which are responsible for fixation of atmospheric nitrogen.^{109,110}

Cyanobacteria are protected from solar UV-B radiation by production of a number of UV-absorbing substances (see section on protective mechanisms above).¹¹¹ Other mitigating strategies include avoidance, colony and mat formation, scavenging of reactive oxygen species (ROS), and repair of UV-induced damage.⁸² In addition, cyanobacteria regulate their position in the water column through buoyancy, by producing gas vesicles.¹¹² When grown only under visible radiation, the filaments of *Arthrospira* maintained their buoyancy, whereas they migrated downwards

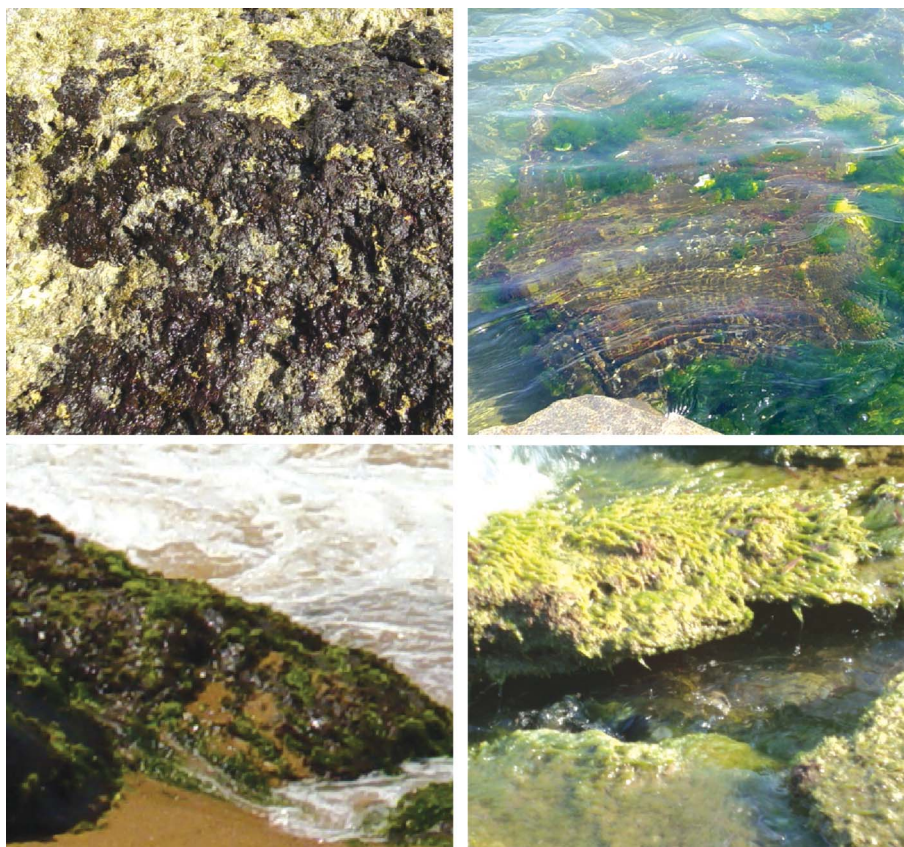


Fig. 3 Typical assemblages of cyanobacteria with other algae in aquatic habitats. Cyanobacteria are major biomass producers in freshwater and marine habitats. They are also important nitrogen fixers for aquatic habitats. Even though they synthesize protective pigments and use other mitigating strategies they are affected by solar UV-B radiation. Courtesy R. P. Sinha.

when UV radiation (280–400 nm) was added. Higher temperatures caused by global climate change may compromise this avoidance strategy under excessive solar UV-B radiation, *e.g.* by decreasing the depth of the upper mixed layer.

In addition to direct cellular damage, solar UV-B radiation can impair cyanobacteria by producing ROS,¹¹³ against which the organisms protect themselves by the synthesis of antioxidants.¹¹⁴ *Nodularia* are dominant cyanobacteria in massive blooms in the Baltic Sea during high levels of solar radiation and stable stratification. The ability to fix nitrogen, tolerance to phosphorus starvation and increased MAA production, demonstrated in an outdoor experiment, may contribute to the competitive advantage over other phytoplankton during blooms.¹¹⁵

Effects of UV radiation on phytoplankton communities

Phytoplankton are one of the main producers in marine systems, synthesizing organic matter *via* photosynthesis and accounting for about half of the production of organic matter on Earth. They absorb large amounts of atmospheric carbon dioxide, some of which sinks to the deep sea floor (see discussion of the “biological pump”).³⁰ Specific effects of UV radiation (particularly UV-B) on DNA,¹¹⁶ carbonic anhydrase,¹¹⁷ fatty acid composition¹¹⁸ and metabolic processes, *e.g.* photosynthesis,¹¹⁹ and calcification¹²⁰ of phytoplankton organisms have been reported.

Specificity of UV radiation effects

The responses of phytoplankton to solar UV radiation exposure have an important component of species-specificity,^{118,121} thus having an impact not only on biodiversity but also on the food web. However, part of the responses and the acclimation potential to light stress, for both PAR (photosynthetically active radiation, 400–700 nm) and UV radiation, are dependent on the previous light history regime imposed on the cells. On the one hand, the light history depends on various climate change factors, such as the changing depth of the upper mixed layer, the water transparency, *etc.*, while acclimation would also depend on temperature. For example, some species are photoinhibited under high UV radiation when previously acclimated to low light, but are then capable of reaching high photoprotection levels when acclimated to moderate-high light. The acclimation mechanisms include interspecific changes in the xanthophyll cycle activity,^{122,123} in MAA concentration¹²⁴ or in superoxide dismutase activity.¹²⁵

When exposed to UV radiation, some diatoms (*i.e.* *Skeletonema costatum*) were very sensitive and did not survive for more than three days, whereas others (*e.g.* *Amphora coffeaeformis* and *Odontella aurita*) were able to acclimate to UV stress, although through different processes.¹²⁶ Differential acclimation of species in relation to their habitat can occur during the spring bloom in some coastal areas.¹²² The acclimation mechanisms, however, are also affected by UV radiation (*e.g.* affecting the xanthophyll

cycle), thus reducing the photoprotective capacity.⁸⁶ In addition, different species use different mechanisms. For example, while one species acclimated relatively fast (3–5 days) to solar UV radiation by synthesizing UV-absorbing compounds,¹²⁷ another species accelerated or upgraded repair processes for UV-induced damage.¹²⁸ The concentration of CO₂ seems to have a role in conditioning the sensitivity of a diatom (*Thalassiosira pseudonana*) as this species was more sensitive to UV radiation when acclimated to high CO₂ than under atmospheric CO₂ levels. Previous acclimation to UV radiation, however, partially counteracted the increased sensitivity observed under elevated CO₂ conditions.^{129,130}

Comparative studies on the swimming behaviour (avoidance strategy) of some phytoplankton species also demonstrated a high variability among species. While some species were insensitive to UV radiation and accumulated near the surface, others were very sensitive to UV-B radiation, decreasing the swimming speed and percentage of motile cells after 2–3 h of exposure to solar radiation. In addition, cells migrate deep in the water column when irradiances are high (local noon).^{131,132} Climate change issues, such as the decreasing depth of the upper mixed layer may change the swimming behaviour as cells may not be able to migrate deep in the water column thus favouring UV-resistant species.

Effects on natural phytoplankton communities

Working with specific cultures, as mentioned above, is important to understand the differential sensitivity and underlying mechanisms for the impacts of UV-B radiation. However, the extrapolation from laboratory results to natural conditions is not direct or simple, and thus working *in situ* and with natural assemblages is preferable. Latitudinal studies have highlighted the variability of phytoplankton responses to solar UV radiation. Studies conducted in the Antarctic showed that open-ocean phytoplankton were more sensitive to UV radiation than coastal assemblages, the latter having higher rates of repair.¹³³ The effects of UV radiation were transient and growth of Antarctic benthic diatoms was generally unaffected, suggesting little or no UV radiation impact.¹³⁴ One contrasting study, however, suggested that the effects of ozone depletion on primary production of Antarctic phytoplankton, in ice-covered and open waters, might not be negative but instead could enhance primary production.¹³⁵ UV radiation induced photoinhibition of natural post-bloom phytoplankton diatom-dominated assemblages from temperate latitudes of Patagonia. The inhibition, however, decreased when samples were dominated by chlorophytes that are potentially a better quality food for grazers.¹³⁹ Tropical phytoplankton assemblages from a coastal site of the South China Sea were significantly inhibited by UV radiation (mostly by UV-B) during sunny days. However, during cloudy days, while small cells (pico- and nanoplankton, <20 µm) were still inhibited by UV radiation, larger cells (microplankton, >20 µm) used UV-A radiation as a source of energy for photosynthesis.¹³⁶ Since climate change would affect cloud cover, this would have a different impact on phytoplankton depending on their size with potential negative implications for the food web.

The importance of small-size cell structure was highlighted in studies carried out in deep ultraoligotrophic lakes in the Andean-Patagonian region where UV-B radiation had a low contribution to photosynthetic inhibition.¹³⁷ In temperate and

tropical environments, artificially added UV-B radiation had a greater inhibitory effect on the synthesis of the D1 protein than on the D1 degradation process itself, thus affecting the synthesis/degradation balance. In addition, the net damage rate of D1 was faster in tropical communities, most likely due to the effects of high light and water temperature.¹³⁸

Estuarine diatoms had a higher and more flexible capacity for photoprotection than oceanic and coastal species, and when exposed to excess light they had less photoinhibition, and thus an adaptive advantage.¹³⁹ Tidal dynamics and physical forcing had important effects on the distribution and photosynthesis dynamics of estuarine phytoplankton. Mixing conditions during low tide, together with relatively high concentrations of DOM and particulate material, result in partial protection for phytoplankton against solar radiation stress.¹⁴⁰ Since both stratification and DOM are affected by climate change (see above), it is not yet clear how the circulation and thus the response of phytoplankton will be affected in estuaries.

Solar radiation affects stoichiometry causing deviations from the carbon : nitrogen : phosphorus (C : N : P) ratio (the Redfield ratio) in phytoplankton, thus changing food quality in aquatic food-webs, as well as affecting biogeochemical cycling.¹⁴¹ High levels of PAR increase C : P ratios in Arctic marine and freshwater phytoplankton species which would likely lower food quality for herbivores. In contrast, exposure to UV radiation reduced cellular C : P (and N : P) ratios in phytoplankton.¹⁴¹ It was suggested that the low C : P ratios in living and dead particles (seston) in the water column are the outcome of an adaptive strategy of algae in environments with high UV radiation exposure and extreme nutrient limitation.¹⁴² Natural plankton communities maintained in mesocosm enclosure experiments (initial CO₂ concentrations of 350, 700 and 1050 ppm) consumed up to 39% more dissolved inorganic carbon at increased CO₂ levels, whereas nutrient uptake remained the same. The stoichiometry of carbon to nitrogen uptake increased from low CO₂ to high CO₂, and this excess carbon consumption was associated with higher loss of organic carbon from the upper layer of the stratified mesocosms.¹⁴³ While the increase in CO₂ concentration would decrease the food quality available for grazers, exposure to UV radiation would tend to counteract this by reducing carbon fixation. Different regions would be affected differently and the balance between these two contrasting effects is still unknown.

Effects of vertical mixing

Studies of the combined effects of vertical mixing and UV radiation have gained increased interest, as mixing affects the radiation field (*i.e.* it produces a fluctuating radiation regime) under which cells are exposed. In addition, increased temperature, as a result of climate change, will affect the stratification of the water column thereby decreasing the upper mixed layer depth, thus affecting mixing and increasing exposure of cells to solar radiation. Fast changing exposure experiments showed significant inter-specific differences in photosynthesis when phytoplankton cells circulated within a simulated upper mixed layer. While one species (*Dunaliella salina*) was affected by both high and low solar irradiances, another (*Thalassiosira weissflogii*) was inhibited only by high solar irradiances. *Heterocapsa triquetra* showed the least variability and benefited from fluctuating radiation regimes.¹⁴⁴

No DNA damage (as measured by accumulation of cyclobutane pyrimidine dimers) was detected in a comparison of three dinoflagellate species (*Heterocapsa triquetra*, *Gymnodinium chlorophorum* and *Prorocentrum micans*) exposed to solar radiation under static and mixing conditions during the austral spring.¹⁴⁵ However, a significant inhibition of photosynthesis was observed in static samples of the three species. Increasing mixing speed increased UV-induced inhibition of carbon fixation in *G. chlorophorum* and *H. triquetra*, but not in *P. micans*. Most of the loss in carbon fixation in *G. chlorophorum* was due to UV-B radiation, while in *H. triquetra* it was due to UV-A radiation. Simulated vertical mixing resulted in more inhibition of photosynthesis by UV radiation as compared to static samples of coastal phytoplankton from the English Channel.¹⁴⁶ Studies carried out with phytoplankton from a tropical, shallow lake in southern China, showed that cells had lower photosynthetic quantum yields under static conditions than under *in situ* conditions in the lake at the same time of the day. During stratified conditions, no impact of UV radiation could be detected *in situ* as compared with the static samples. Increasing vertical mixing not only counteracted the impact of UV radiation but also stimulated photosynthesis.¹⁴⁷ Growth of sub-polar phytoplankton under static and mixed conditions was inhibited by UV-B radiation at the beginning of the experiment (flagellate dominated assemblages) but not after several days of exposure (diatom dominated assemblages). While synthesis of MAAs was the strategy of cells to cope with UV radiation in the fixed-depth experiments, changes in species composition towards more tolerant ones was observed under mixing conditions.¹⁴⁸ Variable mixing conditions together with grazing greatly influenced the algal losses in a freshwater lake.¹⁴⁹

Long-term effects: mesocosm studies

As opposed to short-term experiments (<1 day), long-term experiments using large volumes of samples (mesocosms) provide insight into processes (*e.g.* acclimation, changes in species composition, *etc.*) that need several days to take effect and are often not observed in short-term experiments. Overall, long-term studies point to differential selection of species and food quality, towards UV-tolerant cells. These changes play a critical role that might affect the food chain, although the impact depends on the particular environment considered, thus varying geographically.

Mesocosm studies with phytoplankton from the Gulf of St. Lawrence (Canada), using solar and enhanced UV-B radiation, did not find any effect on phytoplankton biomass or cell concentrations. Bacterial abundances, on the other hand, increased in the enhanced UV-B radiation treatment, due to a reduction of grazing ciliates (*Strombidinium* sp., *Prorodon ovum* and *Tintinnopsis* sp.).¹⁵⁰ Similarly, Antarctic phytoplankton biomass was not reduced by UV radiation, but the species composition was modulated by grazers in the absence of UV radiation.¹⁵¹ At two markedly different sites, one temperate (Canada) and one tropical (Brazil), there was no effect of increases in UV-B radiation on phytoplankton. Attenuation of solar radiation, vertical mixing, and nutrient concentration were the main factors that determined the photoprotection strategies used by the phytoplankton assemblages in these coastal environments.¹²⁴ Experiments carried out with phytoplankton from temperate, tropical, and sub-Antarctic sites showed minor changes in phytoplankton biomass

due to the UV-B radiation; however, changes were significant in UV-B enhanced treatments corresponding to 30% ozone depletion.¹⁵² With high nutrient concentration, phytoplankton photosynthesis was not inhibited by enhanced UV-B radiation, but when nutrients became limiting the sensitivity increased (*i.e.* resulting in net photodamage of photosynthesis reaction centres). Supplemental UV-B radiation also resulted in low abundance of 1,5-bisphosphate carboxylase/oxygenase (RUBISCO, an enzyme involved in carbon fixation during photosynthesis), and increased photoinhibition as compared to the phytoplankton exposed to surface ambient irradiance.¹⁵³ In temperate regions of the South Atlantic the observed changes in species composition were mainly due to nutrient availability, and to a lesser extent to solar UV radiation.¹⁵⁴ Studies conducted in a high-mountain lake in the Sierra Nevada (Spain) suggested that the UV radiation and total phosphorus interactive effect would favour a few UV-tolerant rapidly-growing species.¹⁵⁵ Significant interactive effects of UV radiation and nutrients and UV radiation and DOM were found on phytoplankton when working with natural assemblages from Lake Giles (USA). The differential sensitivity to UV radiation of some species (*Synura* sp. and *Chroomonas* sp.) suggests that changing environmental factors between spring and summer promoted differences in the relative importance of UV radiation in changing phytoplankton community structure.¹⁵⁶ Arctic fjord mesocosm studies suggested that UV-B radiation had the effect of changing the relative biomass proportions of flagellates (*i.e.*, nanoflagellates and choanoflagellates).¹⁵⁷

Productivity of seaweeds under elevated UV radiation levels and global climate change

Seaweeds (macroalgae) are major biomass producers in all oceans from the tropics to polar marine habitats. They provide shelter and food for fish, crustaceans and many other animals, and perform other vital ecosystem functions.¹⁵⁸ In addition, they are exploited for a wide range of products for industry, such as gelling agents, as human foods and a source for vitamins, minerals and phytopharmaceuticals, *e.g.* as antioxidants.^{159–161} *Sargassum* is a potent source of CDOM since it floats on the ocean surface which maximizes its exposure to solar UV.

Even though not immediately endangered by current levels of solar UV-B radiation, the combination with other stress factors such as global warming, increased storm frequencies and pollution, may impact macroalgal canopies, with far-reaching consequences for aquatic grazers and other members of these habitats.

In contrast to phytoplankton, macroalgae are attached to the substratum and therefore cannot escape excessive UV radiation by vertical migration. PAR, and especially UV-B radiation, are major factors in determining the depth of growth, thus controlling the vertical zonation. In the intertidal zone UV-tolerant macroalgae are exposed to extreme variations in temperature, salinity and exposure to solar radiation.¹⁶² Sensitive species are generally limited to greater depths or shaded habitats. Transplantation experiments showed that deep-water, UV-sensitive species do not tolerate being exposed at or close to the water surface.¹⁶³ In intertidal species, DNA damage by UV radiation is lower and repair of DNA damage more efficient than in deep water species.^{164–166} Field

experiments on macroalgal communities on King George Island, Antarctica, demonstrated that increased solar UV-B radiation due to stratospheric ozone depletion may affect the zonation, composition and diversity of Antarctic intertidal seaweeds.¹⁶⁷ Vertical zonation is also determined by species-specific sensitivity of early life stages to solar UV-B radiation.

Most macroalgae undergo life cycles with delicate juvenile developmental stages, which are specifically prone to damage by solar UV-B radiation.¹⁶⁸ Spore germination and attachment of young plants of *Laminaria japonica* were found to be impaired by even low UV-B radiation doses.¹⁶⁹ Also, the early developmental stages of commercially important red and green algae were found to be affected by high levels of solar UV-B radiation.^{79,170} Higher temperatures, such as those expected to result from global climate change, augment UV-B-related damage of early developmental stages.¹⁷¹

One of the major targets of solar UV radiation is the photosynthetic apparatus. Oxygen production, electron transport and quantum yield are affected in red, green and brown algae.^{172–174} In seaweeds, the photosynthetic complexes are reorganized for adaptation to the diurnally changing UV stress.^{175,176}

DNA is another target of solar UV-B radiation.¹⁷⁷ DNA damage is a function of geographical position, depth of growth, water transparency, UV-absorbing pigments and thallus thickness.¹⁷⁸

Macroalgae have developed a number of protective strategies against solar UV-B radiation. In addition to habitat selection, they produce a range of UV-absorbing pigments. While many red algae synthesize MAAs,^{161,179} in brown algae, alginates and phenolic compounds such as phlorotannins provide protection from solar UV radiation.^{180,181} The brown alga, *Sargassum*, uses the carotenoid fucoxanthin for protection from UV-B radiation.¹⁶⁷ In addition, these organisms use repair mechanisms to mitigate DNA damage.¹⁷⁷

Responses of aquatic plants and mosses in freshwater ecosystems to enhanced solar UV-B radiation

Aquatic higher plants and mosses are major biomass producers in freshwater ecosystems and are exposed to UV-B radiation stress. Solar UV radiation impairs photosynthesis as well as respiration in some aquatic plants (*e.g.* *Ceratophyllum*).¹⁸² Experiments with simulated solar UV radiation on aquatic plants, collected in New Zealand from different South Island lakes with different transparencies, indicated that photosynthetic yield was decreased by UV-B radiation stress.¹⁸³ However, surprisingly, in some species the photosynthetic yield was decreased more when UV-B radiation was filtered out of the spectrum. This observation was confirmed by field studies. One possible explanation is that short wavelength radiation may induce recovery processes.

UV-absorption spectra of extracts from a number of mosses and liverworts were analysed from Tierra del Fuego (Argentina).¹⁸⁴ The detected substances were identified as phenolic derivatives, which may be either screening pigments or antioxidants. Those in liverworts were more pronounced than those in mosses.

Physiological responses to solar UV-B radiation have been studied over three years in the aquatic liverwort, *Jungermannia*, growing in mountain streams in northern Spain. Among the variables measured, the photosynthetic quantum yield (decreased)

and the level of UV-absorbing compounds (increased) seemed to be the most responsive to enhanced UV-B radiation.¹⁸⁵ In autumn, newly developed shoots produce significantly higher concentrations of the UV-absorbing pigments than in winter or spring. The best correlation was found between the main UV-absorbing substance (*p*-coumaroylmalic acid) and UV-B radiation stress, reflecting seasonal changes. Because of the high concentrations of the UV-absorbing pigments, hardly any UV damage was detected on vitality, photosynthetic quantum efficiency or chlorophyll concentration, indicating that this liverwort is tolerant to UV radiation.¹⁸⁶ Researchers also tried to correlate the concentration of the UV-absorbing hydroxycinnamic acid derivatives with historic UV radiation levels from 1850 to 2006 using 135 herbarium samples of *Jungermannia* from northern Europe.¹⁸⁷ Both UV absorbance and UV irradiance were positively correlated with the collection year. Because of this high correlation, hydroxycinnamic acid derivatives in this aquatic liverwort have been suggested as potential bioindicators of enhanced solar UV radiation.¹⁸⁶

Effects on aquatic consumers of UV radiation and interactions with climate change

The important role of UV radiation as an environmental stressor has been demonstrated in many aquatic animals with a particular focus on zooplankton, amphibians, fish, and corals. A recent meta-analysis revealed negative effects of ambient UV-B radiation on growth and survival of a wide range of aquatic organisms (not just animals) and concluded that synergisms among multiple stressors are particularly important in the face of global environmental change.¹⁸⁸ There is also some evidence that although UV radiation is generally perceived as damaging, certain levels of solar UV radiation exposure may be beneficial to some consumers.⁵⁵ Here we assess results from recent work on UV radiation effects on animals with a particular emphasis on the sub-lethal and interactive effects of UV with other environmental variables.

Zooplankton

Zooplankton provide a key link in aquatic food webs in lakes and oceans. Their feeding on phytoplankton can alter the transparency of water and simultaneously acts as a conduit of primary productivity to higher levels in the food web including most fish. Some zooplankton such as copepods are also important vectors of human parasites and pathogens.¹⁸⁹ With ozone depletion still a persistent problem at higher latitudes for the coming decades, (see McKenzie *et al.*¹⁹⁰) the potentially damaging effects of UV radiation on zooplankton remain a central concern. A recent paper reviews the different strategies that zooplankton use to cope with UV radiation including photoprotection, photorepair, and behavioural avoidance, and suggests that in general zooplankton are well adapted to existing UV radiation levels.^{18,191} Most of the recent UV work with zooplankton has been on freshwater species, but there have been several studies on marine species as well. The primary findings suggest that UV radiation has the potential to cause damage to some zooplankton through both direct and indirect effects, but many species have effective defences, and a few UV-tolerant copepods may even benefit from moderate UV radiation exposure. This makes it unlikely that the levels of UV radiation predicted for the coming decades will have

direct, large-scale negative impacts on zooplankton in natural waters. The interactive effects of UV radiation with other stressors, including climate change, leave greater cause for concern as they are poorly understood and may have important effects on the role of zooplankton in aquatic ecosystems.

Direct effects of UV on marine zooplankton include reduced survival of UV-exposed larval krill and copepods from Antarctic waters.¹⁹² Indirect effects of UV include production of fewer eggs and more deformed larvae in marine copepods when they are fed UV-exposed *versus* unexposed diatoms.¹⁹³ Freshwater zooplankton are similarly susceptible to UV radiation damage, and sensitivity varies with species, life history stage, and temperature. Field experiments in alpine lakes at 8° and 12 °C found a significant negative effect of ambient UV radiation on juvenile survival and the reproductive state of female copepods at the colder temperature only.¹⁹⁴ Adult survival was not influenced by UV at either temperature. Laboratory experiments with the widespread and abundant freshwater (cladoceran) *Daphnia* also demonstrated a greater sensitivity of juveniles as well as lower reproduction of UV-exposed survivors later in life¹⁹⁵ and cumulative multigenerational effects.¹⁹⁶ This is an important result: rather than prior sub-lethal exposure to UV-B radiation conferring an adaptive advantage to *Daphnia*, it actually magnified the negative effects of UV-B radiation over time. Variable responses to UV radiation by different *Daphnia* species may contribute to the contrasting results. Other sub-lethal effects of UV radiation include significant changes in respiration rates,¹⁹⁷ decreased susceptibility to metal toxicity, increased sensitivity to flouoroanthene (a polycyclic aromatic hydrocarbon, PAH) and the antibiotic sulfathiazole in *Daphnia*,¹⁹⁸ inhibition of acetylcholinesterases¹⁹⁹ and increased production of constitutive heat shock (stress) proteins in copepods.²⁰⁰ In some of the more UV-tolerant copepods, low levels of UV exposure may actually be beneficial, enhancing survival and reproduction,²⁰¹ a result consistent with the positive association of diatomid copepods with high UV environments in alpine lakes.²⁰²

Freshwater zooplankton can also reduce the threat of UV radiation damage through behavioural avoidance, which is generally stronger in cladocerans such as *Daphnia* than in copepods.^{203–205} The behavioural response of *Daphnia* to UV radiation, however, is not influenced by prior exposure to the radiation.²⁰⁶ Field studies in lakes with²⁰² and without²⁰⁷ visual predators suggest that UV radiation plays a role in the daytime vertical distribution of some, but not all zooplankton. While cladocerans show stronger behavioural avoidance of UV, copepods use photoprotection to a greater extent.²⁰⁸ Some freshwater protozoans²⁰⁹ and the larvae of coral²¹⁰ depend heavily on photorepair of their DNA damage.

Zooplankton also reduce UV radiation damage with photoprotective compounds including carotenoids, MAAs, and the antioxidant enzymes catalase (CAT) and glutathione-S-transferase (GST). MAAs have been reported in krill,²¹¹ rotifers²¹² and freshwater²¹³ and marine⁶⁷ ciliates that contain endosymbiotic algae. Symbiotic *Chlorella* in the ciliate *Paramecium bursaria* contain no MAAs, but still confer some UV protection to this ciliate.²¹⁴ Several factors have been found to influence the concentrations of photoprotective compounds in zooplankton including ambient UV radiation exposure levels,^{215,216} temperature,²¹⁷ and visual predators.^{215,216} UV radiation exposure levels in the field were not related to the activity of CAT and GST in two freshwater crustaceans,²¹⁸ but low ratios of phosphorus to carbon in algal

food and UV exposure in laboratory experiments reduce levels of these antioxidant enzymes.²¹⁹

UV influences the interactions of zooplankton with other components of aquatic ecosystems. For example, seasonal increases in UV transparency (UV “clear-water phases”) appear to be induced by photobleaching of DOM by UV radiation and to a lesser extent by zooplankton grazing.²²⁰ UV radiation can also increase feeding rates of planktivorous fish on zooplankton,²²¹ increase degradation rates of chemicals released by predators that induce defences in their zooplankton prey,²²² and contribute to photosensitization of toxic compounds.²²³ Susceptibility to UV radiation of some insect larvae (*Chaoborus*) is species specific.²²⁴

One of the most striking relationships recently observed between UV radiation and zooplankton is the strong reduction in the species diversity of zooplankton in shallower lakes with high UV transparency in Patagonia. Only a single species of highly UV-tolerant copepod persists in fishless lakes with high UV radiation (on average the water column has of UV levels over 10% of incident sunlight measured at 320 nm UV).¹⁹¹ The interactive effects of climate, as well as pH-driven changes in DOM and hence UV transparency of aquatic ecosystems, may be particularly important to the reproduction, survival, and development of early life history stages of even more UV-tolerant copepod species.¹⁹⁴ Modelling suggests that photoinhibition by UV radiation can contribute to destabilization of plankton communities.¹⁹⁵

Amphibians

In recent years there has been an active debate as to the relative importance of UV radiation in widespread declines and malformations in amphibians. The most recent data suggest that a combination of behavioural responses by egg-laying females, physiological tolerance of embryos, reduced water clarity related to DOM concentrations, and timing of oviposition make it unlikely that UV radiation is an important factor for lethal effects in nature.^{225,226} A recent review of the effects of UV-B radiation on amphibian development and metamorphosis emphasizes the importance of looking at sub-lethal effects rather than just mortality.²²⁷ These sub-lethal effects may in turn lead to ecologically important trade-offs in the growth and reproduction of amphibians due to reductions in the ability to exploit optimal thermal habitats or food resources, or minimize exposure to predation. In other cases exposure to UV radiation may increase resistance to some toxic compounds. Complex interactions between UV radiation and other environmental variables seem to be the rule rather than the exception.

One of the sub-lethal effects is the behavioural avoidance of UV radiation. Field surveys and experiments revealed no avoidance of UV-B radiation by three species of anuran tadpoles,²²⁸ but some behavioural avoidance of UV-B in poison dart frogs.²²⁹ Laboratory experiments show that prior exposure to UV radiation increases UV tolerance in larval and juvenile salamanders and that there is high resistance to damage by natural levels of UV radiation.²³⁰ Similarly, a combination of low water transparency to UV radiation as well as to UV-protective compounds in the jelly of egg masses suggest several species of amphibian embryos in Patagonia are not susceptible to UV damage in nature.²³¹ This same study reported no significant effect of UV radiation on survival, but an elevated incidence of malformations with

UV-B exposure when comparing natural and elevated levels of UV-B radiation. Laboratory experiments comparing UV-B tolerance of frog eggs from populations at different elevations (333–2450 m) revealed that UV-B induced a shorter larval body length, with the effect being strongest in eggs collected from low elevations.²³² Field studies of the boreal toad in Glacier National Park, Montana, USA, indicate that UV-B exposure does not limit distribution, and breeding was actually higher in high UV radiation habitats.²³³

UV radiation has important interactive effects with other environmental stressors, including delayed development rates in frog tadpoles when exposed to UV-B radiation and environmentally realistic concentrations of 4-*tert*-octylphenol, an estrogenic microbial decomposition product of widely used industrial surfactants,²³⁴ and a seven-fold increase in lethality of UV-B radiation when toad tadpoles were exposed in the presence of nitrite.²³⁵ There is also some evidence that prior exposure to UV radiation may confer resistance to the interactive effects of UV radiation and toxic compounds, a phenomenon known as co-tolerance. For example, higher levels of UV-B tolerance of tadpoles may confer resistance to the PAH benzo[a]pyrene due to similar genotoxic defences against these two stressors.²³⁶ Higher genetic diversity was also found to confer increased resistance to UV-B-induced mortality and deformity in larvae of wood frogs exposed to natural sunlight with and without UV-B.²³⁷ Frog larvae exposed to artificial UV-B radiation in the laboratory had lower growth rates and more deformities than unexposed larvae, and there was some evidence that they were more susceptible to predation.²³⁸ No synergistic effects of UV-B radiation were observed when three species of anurans were exposed to UV-B radiation and the fungus, *Batrachochytrium dendrobatidi*, which causes chytridiomycosis (an infectious disease).²³⁹ Simultaneous exposure of frog tadpoles (prey) to UV-B radiation from fluorescent lamps and predatory chemical cues significantly increased mortality, and suppressed the predator-induced phenotypic changes that protect against predation.²⁴⁰

Fish

As with many animals, the early life history stages of fish tend to be the most sensitive to UV radiation damage. Enhanced UV-B radiation can reduce growth rates and immune function in juvenile Atlantic salmon,²⁴¹ and increase cataract-causing trematodes (parasitic flatworms) in juvenile rainbow trout.²⁴² The ability to detect and avoid UV radiation exhibited by some juvenile fish such as Coho salmon in outdoor flumes,²⁴³ as well as juvenile black sea bream in laboratory experiments,²⁴⁴ suggests avoidance of UV radiation may reduce the negative effects of UV radiation in nature. Similarly, though the potential for UV radiation damage in the shallow-nesting bluegill sunfish is high, nest locations under the shade of trees or other structures or at deeper depths reduce the actual impact of UV radiation at the population level.²⁴⁵ Larval mortality of bluegill is highest early in the spawning season with $\geq 10\%$ mortality in over a third of the nests.²⁴⁶ Adult fish may also be sensitive to UV radiation damage as indicated by laboratory exposures of adult African catfish to UV-A (366 nm) that resulted in a wide array of biochemical and tissue damages.²⁴⁷ This study is of particular interest because UV-A radiation may also be beneficial in causing repair of DNA damage through photoenzymatic repair (PER), and the importance and extent of

PER differs among freshwater fish species and with UV radiation exposure level.^{248,249} In clear cold-water lakes high UV radiation transparency may reduce invasions by exotic warm water fish species.²⁵⁰

Corals

A recent review of the effects of solar UV radiation on corals suggests that solar UV is an important ecological and evolutionary force in coral reefs, and has been for a long time, that UV radiation effects are limited to shallower reefs, and that the interactive effects of UV radiation and other stressors need consideration.²⁵¹ UV radiation damage in the coral–algal symbiosis can include persistent decreases in photosynthetic efficiency after several days of exposure to UV radiation from lamps in the laboratory,²⁵² and decreases in growth rates in field experiments.²⁵³ Corals have several key defences to reduce UV-radiation damage. Some recent experiments demonstrated that the UV-absorbing properties of coral skeletons can significantly reduce DNA damage in overlying tissues.²⁵⁴ Advances have also been made in assessing the factors that control UV radiation exposure levels in coral reefs. Spatial and temporal variations in CDOM have been demonstrated to be important in regulating the UV radiation exposure levels of corals in the Florida Keys (USA) and Dry Tortugas (USA).²⁵⁵ A combination of remote sensing and radiative transfer modelling has also been used to estimate UV radiation exposure in coral reefs to help assess the role of UV radiation in coral bleaching.²⁵⁶

Other aquatic animals

Recent laboratory studies on the effects of UV radiation on several species of sea urchins have demonstrated structural and DNA damage to spermatozoa,²⁵⁷ developmental abnormalities,²⁵⁸ and reduced PER rates in embryos at lower temperatures.²⁵⁹ The lack of temperature compensation in PER may in part explain the results of a recent *in situ* experiment that found that embryos of an Antarctic urchin were more sensitive to DNA damage and developmental abnormalities than three other species from lower latitudes.²⁶⁰

Other animals for which UV radiation effects have been examined include amphipods, gastropods, and biological control agents, some of which are relevant to human disease ecology. When some amphipods are exposed to elevated levels of UV radiation they show an increase in antioxidant capacity²⁶¹ and respiration rates.²⁶² UV radiation exposure in experimental field studies led to reduced survival of two intertidal mudflat snails.²⁶³ Laboratory studies of juveniles of the snail that is the intermediate host of the human parasite *Shistosoma mansoni* showed that UV-B radiation inhibited feeding behaviour, led to abnormal growths on the head-foot, and increased mortality.²⁶⁴ UV-B radiation from fluorescent lamps with an emission peak of 315 nm inhibits the effectiveness of two strains of *Bacillus sphaericus* used in biological control of mosquito larvae, suggesting that these bacteria need to be used with a photoprotectant, to be maximally effective in the field where solar radiation is high.²⁶⁵ Human pathogens such as the oocysts of *Cryptosporidium parvum* may be susceptible to UV radiation damage, suggesting that decreases in UV transparency of surface drinking water supplies may favour persistence of this parasite.⁵³ Recent doubling of DOM concentrations in aquatic ecosystems

in many parts of Europe and eastern North America^{48–50} may thus reduce UV radiation exposure levels and create surface water environments more favourable to UV-sensitive human pathogens such as *Cryptosporidium*.⁵⁵

Interactions with pollutants and pH

Organisms in freshwater and coastal habitats are exposed to a number of environmental stress factors including anthropogenic contaminants from terrestrial drainage, ice melting and maritime traffic (see related discussions in Zepp *et al.*³⁰). These stresses may have additive or synergistic effects with enhanced solar UV-B radiation challenging growth, reproduction and physiological functions of key members of these aquatic habitats.²⁶⁶ While many toxicological studies have been conducted in the laboratory, field experiments demonstrated the complexity and the difficulty in determining the impact of multiple stressors on aquatic ecosystems.²⁶⁶

Interactive reactions with pollutants

Heavy metals, such as cadmium (Cd), are major stress factors for cyanobacteria, phytoplankton and consumers.^{267,268} Simultaneous application of Cd and UV-B radiation caused a more than 10-fold increase in α -tocopherol, which functions as an antioxidant in cyanobacteria.²⁶⁹ In an aquatic liverwort, DNA damage, caused by UV-B radiation, was augmented in the presence of Cd.²⁷⁰ This was attributed to the inhibition of DNA enzymatic repair mechanisms by the heavy metal. Also benthic communities in a natural stream in the Rocky Mountains (USA) are affected by heavy metal pollution; UV-B radiation had greater impact on the metal-polluted sites than on non-polluted ones.²⁷¹ In freshwater habitats, copper (Cu) and other transition metals are often complexed with DOM. Since the latter is photochemically unstable, solar UV radiation has indirect effects on Cu complexation.²⁷² Irradiation at intensities similar to sunlight decreased Cu complexation in a river, suggesting that increased UV radiation might result in higher Cu toxicity. Increasing Cu concentrations due to photooxidation of DOM resulted in increased mortality of larval fathead minnows.²⁷² Benthic communities from a metal-polluted stream were tolerant of metals, but were more sensitive to UV-B radiation than communities from a reference stream.²⁷³ Experiments with freshwater periphyton indicated that cyanobacteria dominated under high-UV radiation, while diatoms dominated in low-UV radiation treatment. Although the high-UV community had higher tolerance to UV radiation and co-tolerance to cadmium (Cd), they had a fivefold reduction in the pigment, chlorophyll *a*, suggesting that acclimatisation had high metabolic costs.²⁷⁴

Photodemethylation by solar radiation is regarded as the most important biogeochemical sink of methylmercury.²⁷⁵ Dissolved gaseous mercury is released from mercury compounds in the water under photolytic action driven by solar radiation. Removal of UV from the radiation reduced the process by an order of magnitude. In Juam Reservoir, Korea, dissolved gaseous mercury concentrations correlated with UV-A and UV-B irradiances and consequently were higher in spring and summer than in fall and winter.²⁷⁶ In a temperate lake in eastern Pennsylvania (USA) emission of gaseous mercury increased during periods of mixing in spring and autumn and was triggered by solar radiation.²⁷⁷

Degradation products of petroleum compounds were shown to be toxic for a number of test organisms including bacterioplankton.²⁷⁸ Simultaneously, UV irradiation inhibits microbial degradation of petroleum products. Water-soluble crude oil fractions and UV-B radiation were found to have synergistic detrimental effects on a field-collected microplankton assemblage from Ushuaia Bay, southern Argentina.²⁶⁶ Picoplankton appeared to be more affected than nanoplankton, which is attributed to their smaller size. The combination of the water-soluble fraction of crude oil and enhanced UV-B radiation exposure resulted in an exacerbation of these individual effects, demonstrating a synergistic effect of both stresses. In Arctic shallow-water marine habitats, phototoxic effects affect algae and bacteria due to the presence of pyrene, a component of crude oil in the sediments.²⁷⁹ The water-soluble fraction of crude oil is not toxic and may even be beneficial by increasing bacterial activity, but becomes highly toxic under exposure to solar UV-B radiation.²¹² Toxicity of polycyclic aromatic hydrocarbons to a broad range of invertebrates, marine and freshwater fish may increase by a factor between 2 and 1000 when sediments are exposed to UV radiation.²⁸⁰

Interactions with increasing CO₂ concentrations

Acidification of lakes and marine habitats is a major stress factor closely related to climate change and augments exposure of aquatic organisms to solar UV-B radiation.²⁸¹ In the north-eastern Ontario lakes acid deposition is linked with atmospheric sulfur and metal emissions.²⁸² Experimental acidification and recovery of a small lake confirmed the changes in benthic algal communities.^{266,283} The increasingly important role of inland aquatic ecosystems as a reservoir of organic carbon and thus an important link in the carbon cycle have been further strengthened by new studies (see ref. 284 and Zepp *et al.*³⁰)

Decreasing pH of marine waters due to increased atmospheric CO₂ concentrations affects carbonate incorporation in many calcified marine organisms and makes them more vulnerable to solar UV-B radiation. Before industrialization the CO₂ concentration in the atmosphere was about 280 ppm. This corresponded to an average pH in the oceans of about 8.2. The current 380 ppm has resulted in a decrease in pH by about 0.1, which corresponds to a 30% increase in acidity.²⁸⁵ A pH decrease of 0.3–0.4 units is expected by the year 2100. This acidification compromises calcification in molluscs, phytoplankton (Coccolithophoridae) and some macroalgae (*e.g.* *Corallina* and the *Conchoecelis* stage of the Rhodophyte *Porphyra*). Calcium carbonate encrustations efficiently absorb UV radiation. At lower pH values increased transmission has been measured, exposing the organisms to higher levels of solar UV-B radiation.²⁸⁶ UV radiation significantly inhibited growth, photosynthetic oxygen evolution and calcification rates in *Corallina* at high CO₂ concentrations (1000 ppm as compared to 380 ppm).

These results indicate the synergistic effects of lower pH and enhanced solar UV-B radiation in coralline algae. In the coccolithophore, *Emiliania huxleyi*, calcification rates are diminished at lowered pH levels, which result in thinned coccoliths.²⁸⁷ The transmission of detrimental UV radiation was found to be significantly enhanced in enclosure experiments (mesocosms) by acidification by 0.1 pH units.

Interactive effects of UV radiation and climate change at the ecosystem level

As stated in a previous report,¹ "... the ecosystem level [is] where assessments of anthropogenic climate change and UV-related effects are interrelated and where much recent research has been directed. Several studies suggest that the influence of UV-B radiation at the ecosystem level may be more pronounced on community and trophic level structure, and hence on subsequent biogeochemical cycles, than on biomass levels *per se*" (see related discussions in Zepp *et al.*³⁰). These effects not only have implications for marine and freshwater ecosystems, but for the economic and social systems that depend on them. Studies have investigated the effects of solar UV radiation, climate change and their possible interactions, on scales ranging from whole communities to individual organisms at the cellular, biochemical and genetic level. However, there is a paucity of data and information regarding the effects of UV-B radiation on total ecosystem structure and function. Covering new geographical locations and species, most recent studies largely confirm previous findings.²⁸⁸

As an example, the rapid warming of surface waters by 5–6 °C around the Antarctic Peninsula since 1950⁶⁰ has resulted in a shift in species composition that is attributed to deeper migration by organisms in the water column and thus further from exposure to surface UV radiation. These higher surface temperatures have led to later advance and earlier retreat of sea-ice and consequently a shorter sea-ice season.^{60,289} The resulting potentially higher phytoplankton productivity in the area of the Antarctic Peninsula could augment carbon sequestering from the atmosphere through a shift from the invertebrates, such as krill, to an increased population of salps (free-swimming marine chordates of the subphylum Tunicata, having a translucent, somewhat flattened sac-like body).²⁹⁰ Besides krill and copepods (crustaceans), salps are the most important metazoans in that area involved in sequestering carbon from the atmosphere.^{291,292} In the sequestration process, phytoplankton absorb carbon dioxide from the atmosphere *via* photosynthesis. Zooplankton graze on the phytoplankton, and the organic material is packaged into large faecal pellets. These pellets sink to the deep sea floor, and the embedded carbon is removed from circulation for tens of thousands of years, making the area around the Antarctic Peninsula one of the world's most important carbon sinks. In addition, due to the deep migration of the salps in the water column, they are less affected by surface UV radiation. In contrast, other studies demonstrated that any increase in UV-B irradiance would have a negative impact on Antarctic krill because of the relatively shallow descent-ascent migration pattern of their embryos and larvae.¹⁹²

Conclusions

Numerous publications show that solar UV radiation can adversely affect aquatic organisms. The majority of these studies document significant negative impacts on individual species; yet considerable uncertainty remains with respect to assessing effects on whole ecosystems. With respect to assessing UV radiation-related effects, the influence of climate variability is often more important *via* indirect effects such as reduction in sea ice, changes in water column bio-optical characteristics and shifts in limnological or oceanographic biogeochemical conditions than

through direct effects. Were it to occur, decreases in primary production would result in reduced sink capacity for atmospheric carbon dioxide, with its related effects on climate change.

Recent studies have strengthened evidence that the impact of UV-B radiation on phytoplankton is species specific. Acclimation capacity defines the species sensitivity. However, increased stratification (*via* thermal heating or tidal dynamics), together with changes in cloud cover, strongly modifies the light regime and response of phytoplankton. Previous acclimation also counteracts the higher sensitivity of phytoplankton observed when they grow under high CO₂ levels. The carbon uptake is higher at high CO₂ levels, but with the same nutrient uptake, thus increasing the C : N ratio and decreasing the food quality for herbivores. In contrast, exposure to UV radiation reduces cellular C : P ratios (and N : P) in phytoplankton. Therefore, exposure to CO₂ and UV radiation are causing opposite effects on food quality (*i.e.*, phytoplankton C : N ratios). While an increase in CO₂ means a low quality food due to an increase in C uptake, exposure to UV radiation means a better quality food due to a decrease in C uptake.

While zooplankton and many other aquatic animals are often protected from the lethal effects of UV radiation by both their own defences and environmental shielding by UV-absorbing DOM, many recent studies demonstrate the importance of sub-lethal UV radiation effects and interactive effects of this radiation with other environmental stressors. In lakes with high UV transparency, zooplankton communities may be reduced to a single UV-tolerant species,¹⁹¹ amphibians may be more susceptible to toxic compounds,^{234,235} and fish spawning may be limited to shaded or otherwise low UV radiation exposure habitats.^{245,246}

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