

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

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Received 2nd January 2007, Accepted 2nd January 2007

First published as an Advance Article on the web 25th January 2007

DOI: 10.1039/b700020k

Recent results continue to show the general consensus that ozone-related increases in UV-B radiation can negatively influence many aquatic species and aquatic ecosystems (*e.g.*, lakes, rivers, marshes, oceans). Solar UV radiation penetrates to ecological significant depths in aquatic systems and can affect both marine and freshwater systems from major biomass producers (phytoplankton) to consumers (*e.g.*, zooplankton, fish, *etc.*) higher in the food web. Many factors influence the depth of penetration of radiation into natural waters including dissolved organic compounds whose concentration and chemical composition are likely to be influenced by future climate and UV radiation variability. There is also considerable evidence that aquatic species utilize many mechanisms for photoprotection against excessive radiation. Often, these protective mechanisms pose conflicting selection pressures on species making UV radiation an additional stressor on the organism. It is at the ecosystem level 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 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*.

Introduction

Aquatic ecosystems are key components of the Earth's biosphere.¹ They produce more than 50% of the biomass on our planet (Fig. 1) and incorporate at least the same amount of atmospheric carbon dioxide as terrestrial ecosystems (*cf.* Zepp *et al.*²). The primary producers in freshwater and marine ecosystems constitute the basis of the intricate food webs, providing energy for the primary and secondary consumers and are thus important contributors for the production of the human staple diet in the form of crustaceans, fish, and mammals derived from the sea. Solar UV can negatively affect aquatic organisms.^{3–5} The massive loss of stratospheric ozone over Antarctica during the past two decades as well as ozone depletion over the Arctic and high to mid latitudes have aroused concern about the effects of increased solar UV-B radiation on marine and freshwater ecosystems.⁶ Clear lakes and oceans in alpine and polar regions, where UV penetrates deep into the water column, may be particularly vulnerable. The biological organisms in polar waters are even more at risk because of the limited repair capabilities under the inhibitory effects of low temperatures.⁷

Exposure to solar UV radiation can reduce productivity, affect reproduction and development, and increase the mutation rate in

phytoplankton, macroalgae, eggs, and larval stages of fish and other aquatic animals. Consequences of decreased productivity are a reduced sink capacity for atmospheric carbon dioxide and negative effects on species diversity, ecosystem stability, trophic interactions and ultimately global biogeochemical cycles (*cf.* Zepp *et al.*²). In contrast, UV-A, in addition to being deleterious has some positive effects, as it can be used as a source of energy for photosynthesis, or in DNA-related repair mechanisms.

Solar UV radiation and penetration in aquatic ecosystems

A growing number of stations and networks have shown that there has been an increase in solar UV-B radiation at the surface of and within aquatic systems^{8–11} which corresponds with stratospheric ozone depletion.¹² Comparative measurements indicate continued increases in solar UV-B, which are masked by much larger seasonal changes and geographic differences (*cf.* McKenzie *et al.*¹³).¹⁴ Instrument accuracy has been improved in recent years and measurement deviations have been quantified.¹⁵ In addition, biological and chemical actinometers have been developed to determine UV-B doses on site during experiments and exposure.^{16–19}

Aquatic environments vary tremendously in their UV attenuation. Coastal areas and shallow continental shelf waters have a lower transparency than open ocean waters due to the runoff of silt and dissolved organic carbon (DOC) from shores. In open oceans the optical properties are largely determined by plankton and their degradation products,^{20–22} with zooplankton being an additional source of DOC.²³ Owing to the high input of inorganic and decaying organic material, freshwater ecosystems usually

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† This paper was published as part of the 2006 UNEP assessment on environmental effects of ozone depletion and its interactions with climate change.

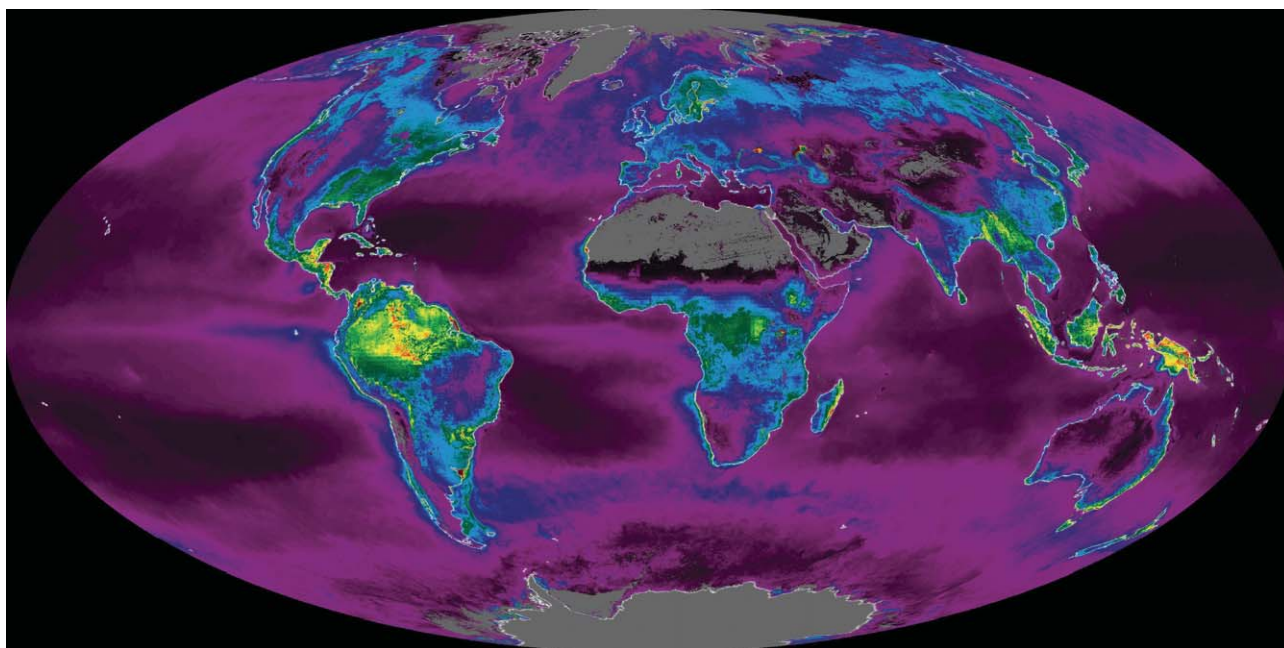


Fig. 1 This false-color map represents the Earth's carbon "metabolism"—the rate at which plants absorbed carbon out of the atmosphere during the years 2001 and 2002. The map shows the global, annual average of the net productivity of vegetation on land and in the ocean. The yellow and red areas show the highest rates, ranging from 2 to 3 kg of carbon taken in per km² per year. The green areas are intermediate rates, while blue and purple shades show progressively lower productivity. In any given year, tropical rainforests are generally the most productive places on Earth. Still, the ongoing productivity near the sea's surface, over such a widespread area of the globe, makes the ocean more productive than the land. (Image courtesy of NASA, 2003).

have a high UV absorption which also depends on their level of eutrophication.²⁴

Ozone and aerosols provide the primary filter in the atmosphere that reduces damaging UV radiation before it reaches the Earth's surface. While stratospheric ozone depletion has now stabilized and is beginning to return to pre-Montreal Protocol levels (see McKenzie *et al.*¹³), the UV transparency of inland aquatic ecosystems remains highly variable and subject to increased UV exposure due to climate change.²⁵ Climate change alters the DOC concentration and hence the UV transparency of inland waters. Warmer, drier climates in particular will reduce the inundation and water saturation of soils within watersheds and hence reduce the inputs of DOC to adjacent lakes and streams.²⁵ In some cases a combination of acidification and climate change has led to dramatic increases in underwater UV penetration²⁵ (see Zepp *et al.*²). The impact of climate change may be particularly pronounced in freshwater ecosystems with low DOC concentrations due to the exponential increase in UV penetration at DOC concentrations below 2 mg L⁻¹ (Fig. 2). Such variable levels of DOC and hence UV exposure may be important factors in determining the distribution and abundance of planktonic and shallow benthic organisms as well as influence the spawning depth of vertebrates such as amphibians and fish that lay their eggs in shallow surface waters.

Climate warming has been found to increase eutrophication in boreal lakes.²⁶ In addition, the export of DOC from boreal peatlands increases with temperature. Since these areas cover about 15% of the boreal and subarctic regions and climate warming is forecast to be most severe at high latitudes, the increasing temperatures are expected to have significant effects

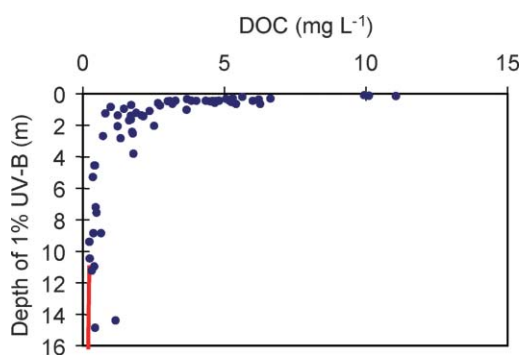


Fig. 2 Relationship between the depth to which 1% of surface 320-nm UV radiation penetrates and concentration of dissolved organic carbon (DOC) in temperature lakes. Note that at low DOC concentrations (1–2 mg L⁻¹) very small changes in the amount of DOC can cause large changes in the depth to which UV penetrates. Adapted from Williamson and Zagarese.²⁵

in boreal areas.²⁷ Phytoplankton abundance may vary by orders of magnitude driven by future climate-DOM-UV radiation interactions.²⁸ Other aquatic ecosystems also show that CDOM (colored dissolved organic material) is a mediator of climate-UV interactions.²⁸ Global warming has not only the potential to affect lake species compositions,²⁹ but also to increase the invasion potential by imported species.³⁰

Besides inorganic particulate matter, dissolved and particulate organic carbon (DOC and POC) are the main attenuating substances in freshwater and coastal marine waters.³¹ DOC concentrations often show large spatial and temporal variability.³² Recent models analyzing the absorption of the components show

that DOC mainly attenuates UV-B radiation while POC mainly decreases the UV-A radiation in the water column.³³ The optical effects of zooplankton and phytoplankton on UV attenuation in freshwater ecosystems are usually low,³⁴ but bacterioplankton plays a major role (*cf.* Zepp, *et al.*²). While DOC is only slowly degraded in the water column, it is readily fragmented by solar UV to smaller subunits,³⁵ which are consumed by bacterioplankton.³⁶ This increases the UV transparency of the water column³⁷ where the resulting deeper UV-B penetration affects bacteria and other organisms.³⁸ In addition, photobleaching increases UV transparency. Increasing temperatures associated with global climate change are generally expected to decrease DOM concentrations and thus increase the penetration of UV-B radiation into the water.³⁹

DOC is a source of dissolved CO₂ in the water,^{40,41} and pCO₂ is closely related to the DOC concentration in Swedish boreal lakes.⁴² Acidification also decreases DOC concentrations.^{43,44} Depending on its concentration, DOC can have positive or negative effects on phytoplankton growth. Low concentrations contribute to nutrient recycling (N and P)⁴⁵ and availability, while higher concentrations negatively affect phytoplankton growth by shading.⁴⁶ Bacteria are the main agents for the mineralization of N and P from DOC. In addition to biomineralization, phototransformation alters biodegradation to a variable degree, depending on the source of DOC.⁴⁷

Arctic and Antarctic marine and freshwater ecosystems are additionally affected by snow and ice cover. Even thin layers of snow or ice significantly decrease the penetration of solar UV.⁴⁸ Earlier ice melting due to increased temperature will expose phytoplankton blooms to higher solar UV radiation. The seasonal change in sea-ice cover is a major determinant of the Antarctic aquatic ecosystem. In addition, glacial meltwater plumes play a critical role near the ice edge and their influence extends more than 100 km into the open ocean and influences the biota by water column stratification, changes in turbidity, salinity and temperature.⁴⁹ Global warming at higher latitudes may lead to shallower mixed-layer depth, more intense seasonal stratification with shallower mixed layers and subsequent influence on UV impact on aquatic ecosystems.

Plankton

Plankton can be subdivided, based on physiological or taxonomic criteria into major groups of bacterioplankton, phytoplankton (including cyanobacteria and eukaryotes) and zooplankton.⁵⁰ In aquatic ecology, size (on a logarithmic scale) is used as a subdivision criterion: femtoplankton (0.02–0.2 μm), picoplankton (0.2–2 μm), nanoplankton (2–20 μm), microplankton (20–200 μm) and macroplankton (200–2000 μm). Even though the smallest organisms contribute a significant share to aquatic biomass productivity, these taxa have not yet been studied extensively in terms of UV sensitivity.

Bacterioplankton and viruses

Although the bacteria are small in size, they contribute a significant biomass component in aquatic ecosystems and play a key role in biogeochemical processes.⁵¹ Predation is the major mortality factor for planktonic bacteria.⁵² Most bacterioplankton

do not produce screening pigments but overcome solar radiation stress by fast cell division and effective repair mechanisms.⁵³ As long as the repair keeps up with the damage, the population is not threatened; but when CPDs (cyclobutane pyrimidine dimers) accumulate under high solar radiation, the population decreases. CPDs constitute by far the most frequent DNA damage induced by UV-B, followed by single- and double-strand breaks.^{54,55}

DNA damage correlates strongly with the penetration of UV radiation into the water column, and UV-B has a stronger effect than UV-A. When bacterioplankton was exposed in UV-transparent bags in tropical coastal waters, DNA damage was detectable down to 5 m. However, inhibition of leucine and thymidine incorporation, as markers for protein and DNA synthesis, respectively, occurred to a depth of 10 m.⁵⁶ Photorepair by the enzyme photolyase, using UV-A/blue light as an energy source,⁵⁷ is a major mechanism to reduce the CPD load.⁵ Alternatively CPDs can be repaired by nucleotide excision repair.⁵⁸ Because of the path length of penetration, size seems to be a decisive factor for UV sensitivity: bacterioplankton from several boreal lakes in Canada were more sensitive to solar UV than the larger phytoplankton.⁵⁹

Phytoplankton density significantly influences the depth distribution of bacterioplankton in the water column. During the summer, dense diatom phytoplankton populations develop in the Antarctic waters off the British Rothera Station, causing strong UV attenuation in the top layers.⁶⁰ At the surface, bacterioplankton incurred large UV-B-induced DNA damage (exceeding 100 CPDs per megabase pairs, Mbp), but it was protected from solar UV-B below the diatom population. This phenomenon was particularly prominent during January and February, when sea ice melting causes pronounced stabilization of the water column. Later in the season, this effect weakened and DNA damage was homogeneously distributed throughout the top 10 m in well-mixed waters.

Solar UV has a decisive role in bacterioplankton community structure in marine surface waters.⁶¹ Large differences in sensitivity were found between different samples from the northern Adriatic Sea. When exposed to UV-B radiation, inhibition of amino acid incorporation varied substantially and there were even larger differences in the efficiency of recovery between species. In Antarctic marine bacteria UV-B and UV-A had similar negative effects on survival.⁶² In contrast, in a high mountain lake (Spain) UV-A exerted the main effect.⁶³ In the upwelling zones of the Humboldt Current System, PAR induced a significant inhibition of bacterial productivity followed by UV-A and UV-B.⁶⁴

Both in the Arctic and Antarctic, spores of *Bacillus subtilis* were inactivated by solar radiation within hours. However, a covering of *ca.* 500 μm of soil or dust or a retreat of ~1 mm into endolithic habitats prevented inactivation of the spores.⁶⁵ Snow covers of 5–15 cm thickness attenuated UV penetration by a factor of 10 and protected the spores from inactivation. Crust formation and biofilms are additional protective measures against environmental factors including desiccation, temperature changes and solar UV.⁶⁶ Halobacteria, being Archaea, show a much higher resistance to solar UV radiation than bacteria and even tolerate UV-C radiation,⁶⁷ reflecting the tolerance of shorter wavelengths penetrating through the atmosphere during early evolution of these organisms. At present UV-C does not reach the Earth surface—except high mountain locations—due to complete absorption in the atmosphere.

Another decisive factor for bacterial communities is the concentration of viruses.⁶⁸ Virus-to-bacteria ratios were found to be lowest in freshwater lakes and highest in saline lakes. The viral abundance was closely correlated with the concentration of DOC. Viruses have neither effective sunscreens nor photorepair capabilities⁶⁹ and are prone to solar UV damage.⁷⁰ This is supported by their seasonal abundance in central European lakes.⁷¹ However, while being sensitive to solar UV, it is surprising that the presence of viruses can provide some protection from solar UV to their phytoplankton hosts such as *Phaeocystis*; the reason for this unexpected phenomenon is not known.⁷² Anthropogenic pollutants such as cosmetic sun screens increase the abundance of viral particles in the water.⁷³

Picoplankton

Unicellular picophytoplankton such as *Synechococcus* and *Prochlorococcus* are recognized as ubiquitous organisms of oceanic microbial loops and as the most abundant marine primary producers.⁷⁴ The effects of ambient levels of solar radiation on oceanic picoplankton were studied in the water column⁷⁵ using the range from unattenuated radiation to 23% of the surface level. The radiation significantly increased cell death in *Prochlorococcus*, while the cyanobacterium *Synechococcus* had ten times the survival rate. Removal of UV radiation strongly reduced the cell death rate in the first species and eliminated it completely in *Synechococcus*. Natural solar radiation decreased the half-life times of the cells to a little over a day. A similar differential sensitivity of the two groups was found for Mediterranean ecotypes.⁷⁶ This generally high sensitivity of picoplankton to ambient solar radiation may act as a primary driver of species composition and population structure and govern the dynamics of the microbial food web in clear oceanic waters.⁷⁵

Natural levels of solar UV-B have been determined in the Red Sea using a DNA biosimeter.⁷⁷ In parallel, depth profiles of DNA damage were analyzed in plankton samples that had been collected from the water column down to 50 m. While the dosimeter did not show any response below 15 m, CPD DNA damage could be found in all plankton samples. CPD concentrations increased during the day and decreased over night, indicating DNA repair, but the dark repair processes did not remove all CPDs during the night. Exposure to UV-B increases the membrane permeability as shown in *Nannochloropsis*, which decreases the nitrogen uptake capability.⁷⁸

Cyanobacteria

During the early Precambrian era, fluxes of solar UV-B and UV-C at the surface of the Earth were several-fold higher than today due to the lack of oxygen in the atmosphere and the consequent absence of ozone in the stratosphere (*cf.* McKenzie *et al.*¹³). Early evolution was therefore limited to UV-protected aquatic habitats. Nonetheless, there was a strong selection for protective and mitigating strategies of early organisms against solar UV radiation.^{79,80} The early UV screens in aqueous environments may have been simple aromatic organic molecules, which later developed into specialized UV absorbers still found in cyanobacteria as well as in some eukaryotic photosynthetic organisms.⁷⁹

Cyanobacteria are major biomass producers both in aquatic and terrestrial ecosystems and represent more than 50% of the biomass in many aquatic ecosystems.⁷⁹ Because of their nitrogen-fixing capacity they serve as important fertilizers both in the sea and in terrestrial plant habitats such as tropical rice fields. Some cyanobacteria produce highly toxic substances, including neurotoxins and peptide hepatotoxins, which cause animal poisoning in many parts of the world⁸¹ and pose considerable risks for human health by polluting drinking water reservoirs and recreational areas.⁸² In the Baltic Sea the filamentous *Nodularia* forms extended blooms in late summer during calm weather.⁸³ These organisms are tolerant of ambient solar UV-B levels and outcompete more sensitive organisms even though solar UV-B has increased by 6–14% over the last 20 years in this area.⁸⁴

Recent studies show that UV-B radiation treatment results in a wide range of responses at the cellular level, including motility, protein biosynthesis, photosynthesis, nitrogen fixation and survival in cyanobacteria.^{85,86} The molecular targets include DNA and the photosynthetic apparatus.^{87,88} The phycobiliproteins, which serve as solar energy harvesting antennae, are specifically bleached by UV radiation.^{89,90} However, several studies have demonstrated an adaptation to UV stress and an increased resistance.^{91,92} Long-term exclusion of solar UV decreased the photosynthetic competence.⁹³ Adaptive mutagenesis, which has been found in cyanobacteria, increases their resistance to UV-B.⁹⁴ Additional stress by exposure to heavy metal ion pollutants adds to the UV-B effect.^{95,96}

Recent studies show that UV-B radiation treatment results in a wide range of responses at the cellular level. On the molecular level UV exposure causes a wide range of responses. It induces an increased Ca²⁺ influx *via* L-type calcium channels.⁹⁷ The stress signal is subsequently amplified and transmitted using cyclic nucleotides as secondary messengers⁹⁸ followed by the production of shock proteins. UV-B treatment increased the concentration of 493 proteins out of 1350 at least threefold in the terrestrial species, *Nostoc commune*.⁹⁹ In addition to direct UV-B-induced damage to the DNA, oxidative stress (singlet oxygen and superoxide radicals) and damage were reported, causing lipid peroxidation and DNA strand breakage.¹⁰⁰ After prolonged UV-B exposures an adaptation to the reactive oxygen species (ROS) stress has been observed.¹⁰⁰ Typical ROS quenchers such as ascorbic acid, *N*-acetyl-L-cysteine or sodium pyruvate have protective effects.^{101,102}

Protective and mitigating strategies of cyanobacteria include mat or crust formation,¹⁰³ vertical migration of individuals within the mat, or self shading due to changes in morphology as observed in *Arthrospira platensis*.¹⁰⁴ In microbial mats the surface layer often serves as a protector for the organisms underneath. A mat in a high Arctic lake showed high concentrations of photosynthetic pigments in the lower part of the mat, while the black top layer was rich in scytonemins and MAAs.¹⁰⁵ By producing UV-absorbing substances including MAAs and/or scytonemins, many cyanobacteria are able to withstand excessive solar UV radiation.^{106–108} MAAs are water-soluble compounds and have absorption maxima in the range from 310 to 360 nm.⁷⁹ Upon absorption of UV radiation MAAs form triplet states which thermally relax and thus render the radiation energy harmless.¹⁰⁹ MAAs are either constitutive elements within the cells or are induced by solar radiation.¹¹⁰ In many cases action spectroscopy has shown that solar UV-B (which peaks around 300 nm) induces MAA synthesis in algae and phytoplankton, while visible

radiation has no effect.¹¹¹ Biosynthesis of scytonemin is induced by exposure to UV-A radiation and can be enhanced by elevated temperatures and photooxidative conditions.¹⁰⁶ Scytonemins are exclusively synthesized by cyanobacteria and are chemically very stable. They can accumulate in sediments; their abundance in sediment cores has been utilized to reconstruct variations in the light regime over time.¹¹² Natural populations of the same species may vary in their concentration, indicating genetic differences.¹¹³

Phytoplankton

Phytoplankton are by far the major biomass producers in the oceans, and form the basis of the aquatic food webs. Their productivity rivals that of all combined terrestrial ecosystems. Another key ecological factor is that phytoplankton contribute significantly to the biological pump: atmospheric carbon dioxide is taken up by primary producers in the sea and is cycled through primary and secondary consumers. Most of this carbon dioxide returns to the atmosphere, but part of this sinks to the ocean floor as zooplankton fecal pellets and, to a larger extent, as dead phytoplankton.¹¹⁴ In effect the biological pump removes about 3–4 Gt of carbon per year from the atmosphere and partially offsets anthropogenic input of carbon from fossil fuel burning and tropical deforestation.¹¹⁵

Phytoplankton are not evenly distributed in the oceans but dominate in the circumpolar regions and the upwelling waters over the continental shelves, as seen by satellite imaging.¹¹⁶ Estimated cell density differences are in reasonable agreement with measurements in the field.¹¹⁷ Marine phytoplankton are dominated by small-sized cells of <2 µm diameter.¹¹⁸ A large number of recent studies points to a considerable sensitivity of phytoplankton communities to solar UV, ranging from polar to tropical habitats.¹¹⁹

Besides limitations in nutrients, light availability, pH and non-permissive temperatures, degree of adaptation and grazing pressure, high levels of solar radiation inhibit photosynthesis in species of different taxonomic groups.^{120–123} The UV component adds more to photoinhibition than its energy share in solar radiation.¹²⁴ This inhibition can be monitored in terms of oxygen exchange,¹²⁵ carbon acquisition¹²⁶ or by measuring the quantum yield using pulse amplitude modulated (PAM) fluorescence.¹²⁷ Nutrient (mainly nitrogen and phosphorus) starvation often augments the UV effects on photosynthetic performance,¹²⁸ but may affect various species to a different degree causing changes in community structure.¹²⁹ This effect of nutrient deficiency may be caused by less efficient repair processes.¹²³ In addition, nutrient uptake, such as phosphorus, may be impaired by solar UV radiation.¹³⁰ Pollutants such as tributyltin, a constituent of antifouling paints, have a synergistic negative effect.^{131,132}

Photorepair is limited at low temperatures. While at 6 °C solar UV radiation significantly inhibited growth in natural phytoplankton samples from a mountain lake in the USA, no such inhibition was observed at 14 °C, indicating that the repair processes compensate the UV inhibition at the elevated temperature.¹³³

Experimentally, ozone depletion has been mimicked by adding supplementary UV radiation from lamps to ambient solar radiation. This approach was tested at three locations in Southern Brazil, Canada and Patagonia.^{134,135}

Photoinhibition in terms of photosynthetic quantum yield is linked to the same mechanism as in other eukaryotic photosynthetic organisms from algae to higher plants: the photosynthetic electron transport chain is disrupted by photodegradation of the D1 protein in Photosystem II.^{136,137} Low visible radiation enhances the repair efficiency while high PAR enhances the damage.¹³⁸ Inhibition of protein synthesis results in retarded recovery. Nutrient starvation limits recovery also.¹³⁸ In contrast to photosynthesis, respiration is less affected by ambient levels of solar UV radiation.¹³⁹

Exposure of natural Antarctic marine plankton to UV at depths from 1 m to less than 20 m showed that some phytoplankton species died, some flourished and others showed no effect.¹⁴⁰ These and other results suggest that ozone-related enhanced UV-B may change food web structure and function which in turn may affect biogeochemical cycles.¹⁴¹ In Canadian Rocky Mountain lakes solar UV-A and UV-B were found to decrease algal density and alter community composition.¹⁴² However, some studies indicated that after long-term exposure to solar UV, phytoplankton can adapt to the radiation.¹⁴³ UV-A had a higher impact than UV-B on hard-bottom shallow marine communities, but the effects on diversity and biomass disappeared during species succession within a few months.^{6,144} Also, in Patagonian oceanic plankton assemblages, UV-A had a stronger effect on photosynthesis during bloom periods than UV-B.¹⁴⁵ However, the relative sensitivity of phytoplankton to UV-A and UV-B may depend on the species composition and the nutrient state.¹⁴⁶ Mixing is an important factor in plankton survival. In contrast to marine habitats with high mixing, lakes often show stable thermal stratification. Consequently, lake plankton communities show vertical distribution¹⁴⁷ and populate certain horizontal bands of optimal light conditions¹⁴⁸ using buoyancy and active motility for niche selection. In the subtropical lake Tanganyika, phytoplankton were affected by solar UV radiation only in the top half-meter, reducing photosynthetic rates, damaging DNA (CPD formation) and inducing UV-absorbing compounds, indicating that vertical mixing decreases solar UV effects by transporting the cells to depth where active repair can take place. Fast vertical mixing within the upper mixing layer of tropical marine environments can enhance photosynthesis. Under cloudy conditions UV-A can be used as a source of energy, while under slow mixing and cloudless skies UV-A is inhibitory.¹⁴⁹ Other targets of UV-B damage are changes in ultrastructure and pigment concentration and composition.^{150,151} Besides direct effects on cellular targets, UV-B also operates *via* the production of ROS.¹⁵² Phytoplankton defend themselves by activating antioxidant systems. However, UV-B decreases the activity of antioxidant enzymes and ROS scavengers.¹⁵³

One mechanism of photoprotection against high solar radiation in many algal species (except red algae) is the xanthophyll cycle, which relies on the thermal dissipation of excess excitation energy thereby reducing the formation of singlet oxygen in the chloroplasts.¹⁵⁴ Zeaxanthin formation is also involved in increased non-photochemical quenching based on the migration of electronic excitation energy from Photosystem II chlorophyll to nearby carotenoids. UV exposure can enhance this process.¹⁵⁵

MAAs are effective UV screens that protect phytoplankton from high solar UV radiation.¹⁵⁶ In the English channel MAAs are present on a year round basis with concentrations increasing rapidly during spring often coinciding with the appearance of

algal blooms.¹⁵⁷ The action spectrum for MAA synthesis induction shows a clear maximum in the UV-B range.¹⁵⁸ In the dinoflagellate *Scrippsiella*, daily vertical migrations have been found to be related to circadian MAA biosynthesis.^{159,160} In dinoflagellates, MAAs seem to be packaged in certain organelles probably increasing the protective efficiency for specific cellular targets.¹⁶¹ MAAs can operate both as UV absorbers and as quenchers for oxidative stressors.^{162,163} While MAAs are very stable molecules with respect to extreme temperatures, pH and UV radiation, they are easily destroyed in water in the presence of photosensitizers.¹⁶⁴

Some freshwater yeasts represent a small group of planktonic organisms showing both a constitutive and a UV-inducible synthesis of photoprotective carotenoids and mycosporines.^{165–167} The specific MAA is a compound linked to a glutaminol-glucoside,⁷⁶ which is also accumulated by copepods and ciliates from their diet.¹⁶⁷ Some green algae in extreme UV environments (snow algae) use sporopollenin as a UV-absorbing substance.¹⁶⁸ Others rely on massive accumulations of carotenoids such as astaxanthin¹⁶⁹ or β -carotene,¹⁷⁰ which provide protection against oxidative stress by scavenging singlet oxygen or peroxy radicals.¹⁶¹

Some phytoplankton taxa including dinoflagellates and diatoms produce toxic substances, such as neurotoxins and domoic acid, and are a severe threat to animals and humans when they form blooms. Recent blooms of the toxic *Pseudo-nitzschia* have caused mass mortality among dolphins, sea lions and birds along the Californian coast.¹⁷¹ These blooms seem to be increasing in frequency and geographical range. The organisms have a low sensitivity to solar UV radiation and escape damage of their photosynthetic apparatus by switching to heterotrophic growth.

Several taxa of marine phytoplankton such as Prymnesiophyceae and some dinoflagellates produce dimethylsulfoniopropionate (DMSP) which is converted into dimethylsulfide (DMS) (*cf.* Zepp *et al.*²). The latter is emitted into the atmosphere and forms cloud condensation nuclei, thereby affecting local climate over the ocean.¹⁷² Cleavage of DMSP is induced by mechanical or dark stress, by grazing or viral attack.¹⁷³ This indicates that DMSP is involved in coping with oxidative stress.^{174,175} Because of the pronounced vertical migrations of the dinoflagellates, diurnal patterns were recorded in DMS production in the St. Lawrence Estuary. Recently, lakes and estuaries have also been found to be important sources of DMS.¹⁷⁶ A model has been developed to simulate the seasonal patterns of DMS production and validated against nutrient concentrations, biological standing stock and other parameters.¹⁷⁷ Marine biogenic iodocarbon emissions are also significant for marine aerosol formation and have a key effect on global radiative forcing.¹⁷⁸ Besides changes in stratospheric ozone, cloud cover is a major factor controlling the exposure of organisms to solar UV.¹⁷⁹

The sea-ice ecosystems in the circumpolar oceans and water bodies of the Baltic and Caspian Seas constitute some of the largest biomes on Earth.¹⁸⁰ The semisolid ice matrix provides niches in which bacteria, phytoplankton algae, protists and invertebrates thrive.¹⁸¹ Those organisms are strongly affected by temperature, salinity, nutrients, visible and ultraviolet solar radiation.¹⁸² Sea-ice phytoplankton provide the fundamental energy and nutritional source for invertebrates such as krill in their early developmental stages which amount to about a quarter of the biomass production in ice-covered waters. The extreme conditions of their habitat force the organisms to adapt physiologically. The production of

large concentrations of MAAs is also essential for the survival of primary consumers which ingest and incorporate the MAAs for their own protection. The expected loss of about 25% of the sea ice due to global warming over the current century will certainly affect the productivity of the polar oceans.¹⁸²

Anthropogenic acidification of boreal lakes decreases resistance of organisms to UV radiation and affects species composition with increasing trophic level. Therefore it is assumed that loss in species diversity will increase the susceptibility of acidified lakes to other stress factors. Ecosystem stability in boreal lakes is thus likely to decline as global change proceeds.¹⁸³

Experiments in large (volume > 1 m³) outdoor enclosures, called mesocosms, are useful for the study of complex impacts on food-web structure and dynamics.^{184–186} Mesocosms permit well-controlled experiments with natural phytoplankton communities in physical, chemical and light conditions mimicking those of the natural environment. In addition, UV radiation within mesocosms can be manipulated to simulate various levels of ozone depletion. Belzil and coworkers¹⁸⁴ find that while UV radiation increases can have subtle effects on bulk biomass (carbon and chlorophyll), changes in community structure may be a more significant ecological effect, because of differential sensitivity to UV radiation among planktonic organisms. These workers note that “planktonic communities do not suffer from the catastrophic negative impacts that might have been inferred from some laboratory experiments on individual components of the marine food web”. They note, in agreement with previous observations, that ambient levels of UV radiation already have significant effects. Mesocosm experiments, including both plankton and their grazers, also suggest that changes in community structure are potentially more important than effects on overall algal biomass.¹⁸⁶ Other workers found that phytoplankton growth was inhibited by UV radiation in fixed-depth experiments but not in mesocosms where vertical mixing exposed planktonic organisms to variable radiation regimes.¹⁸⁷ A synthesis model simulating mesocosm experiments suggests that enhanced UV-B could cause “a shift from primary producers to bacteria at the community level”.¹⁸⁸ Such a shift in community structure could have important consequences for CO₂ levels in oceanic surface waters. A mathematical model based on a predator–prey scheme considers sedimentation of phytoplankton, vertical mixing, and attenuation of PAR as well as UV radiation in the water column. Surprisingly, higher inhibition by UV radiation and longer mixing periods can induce strong fluctuations in the system and enhance plankton productivity due to the stronger effects on the predators.^{189,190}

Macroalgae and aquatic plants

Macroalgae are major biomass producers on rocky shores and continental shelves. The macroalgae canopies form habitats for larval fish, crustaceans, and other animals. Macroalgae are of commercial importance and are harvested on a large scale from natural vegetation and aquaculture for human consumption and industrial use.

Even without ozone depletion, UV-B radiation constitutes a significant stressor for macroalgae. Exposure to solar UV-B results in a host of biological effects on the molecular, cellular, individual and community levels.¹⁹¹ Macroalgae are stressed by solar UV radiation to an extent which is genetically determined and results

in a pronounced vertical stratification.¹⁹² Even closely related species of the same genus may have significantly different UV sensitivity, causing them to grow in different habitats.¹⁹³ UV-tolerant species populate the tidal zone, while more sensitive species are found in deeper waters.¹⁹⁴ Seasonal changes in UV and visible radiation also result in a pronounced succession of species over the year in marine macrobenthic communities.¹⁹⁵ Besides changing salinity, temperature and desiccation in their habitats,¹⁹⁶ macroalgae are exposed to extreme variations in light intensity due to daily, seasonal and tidal cycles as well as changing turbidity in the water column.¹⁹⁷ Intertidal macroalgae of all major taxa can rapidly adapt to fast changes in radiation.^{198,199} Environmental conditions can be extreme in macroalgal habitats where, at polar growth sites, species have to survive in total darkness during several winter months.²⁰⁰

Young specimens were more prone to UV inhibition of photosynthesis, and species collected shortly after the winter were found to be affected more than those harvested later in the year, indicating an adaptive strategy to increasing natural short-wavelength radiation.²⁰¹ Both Arctic and Antarctic species showed pronounced effects of solar UV-B on photosynthesis, morphology and growth rates.^{202,203} Unfiltered solar radiation proved lethal to several Antarctic deep water algae. While tropical macroalgae are better adapted to higher solar UV and visible radiation than higher-latitude species, they are also affected by ambient solar UV.²⁰⁴ Both UV-A and UV-B decrease growth rate, quantum yield of photosynthesis and cause accumulation of DNA damage. Since different species show different sensitivities, increases in solar UV-B radiation could influence species recruitment in the upper intertidal zone.²⁰⁵

Excessive solar radiation causes photoinhibition of photosynthesis;²⁰⁶ elimination of total UV or UV-B alone reduces the severity of photoinhibition and shortens recovery time in many species.^{154,207,208} Electron microscopy revealed pronounced damage of the thylakoid structure.²⁰⁹ Enzymes involved in the photosynthetic CO₂ fixation and sugar formation are affected by UV radiation and the concentration of chlorophyll *a* decreases.^{210,211} The photosynthetic accessory phycobiliproteins operating as antenna pigments in red algae are even more sensitive to solar UV radiation.²¹² UV-B is more effective than UV-A in decreasing growth rate.²⁰⁵ In a laboratory study exposure to UV resulted in significant release of organohalogenes from several polar macroalgae. These substances have ozone-depleting characteristics and so potentially enhance the incidence of solar UV.²⁰⁵

Most macroalgae have an efficient photorepair system of UV-induced CPDs.²¹³ Besides DNA repair mechanisms, efficient ROS scavenging enzymes were found in many macroalgae.²¹⁴ In several Arctic algae these enzymes vary significantly in activity over the growing season when algae have been collected before, during and after break-up of sea ice.²¹⁵ UV sensitivity decreases with age and developmental stage of macroalgae. The germination capacity of zoospores from five Laminariales species were found to decrease sharply after 16 h of exposure to visible and UV radiation.²¹⁶ Both zygotes and young germlings of brown algae show massive inhibition; UV-B radiation is more effective than UV-A.²¹⁷ Also juvenile stages of red and green algae showed a pronounced UV sensitivity.²¹⁸ Both UV-A and blue radiation reactivate spore germination after UV-B inhibition, indicating

photolyase activity.²¹⁹ Motile gametes of brown algae use light-directed movement (phototaxis) to accumulate at the water surface improving the chances of finding a mating partner, but that phototactic response is drastically inhibited by solar UV. Enhanced levels of solar UV-B may affect this vital strategy and thus impair development of kelps.²²⁰

Many macroalgae of the tidal zone produce UV-absorbing compounds while subtidal species usually do not have this protection. However, deep-water algae are rarely exposed to significant levels of solar UV radiation.²²¹ Red algae have the highest percentage of species that synthesize MAAs,²²² followed by brown and green algae. The protective effect of MAAs was shown in the red alga *Porphyra*, commercially sold as Nori, where they block thymine dimer production.²²³ MAAs are very stable against elevated temperatures and UV exposure.²²⁴ The presence of ammonium increases the accumulation of MAAs. The blue component of visible radiation has the highest effect in inducing MAA biosynthesis in *Porphyra*.²²⁵ Polychromatic action spectra of induction reveal the efficiency of short wavelength radiation in several species.^{226,227} Recently a new group of MAAs absorbing at 322 nm has been identified in green algae.²²⁸ The common sea lettuce, *Ulva*, was found to produce a UV-B absorbing compound with a maximum at 292 nm.²²⁹ In brown algae a novel group of UV-absorbing pigments, phlorotannins, has been found.²³⁰ Macroalgae can be classified according to their MAA production. Most deep water algae never produce MAAs even when transplanted to surface waters. Algae from the intertidal zone often show induction of MAAs, while species growing near the water surface normally have a high concentration of MAAs, which cannot be further induced.²³¹ Other defense mechanisms against photooxidative stress involve the induction of a wide range of antioxidant enzymes in brown, green and red algae²³² as well as biosynthesis of several carotenoids.²²⁶

Aquatic mosses and liverworts show UV-B-related responses similar to those of many macroalgae, including inhibition of photosynthesis, growth and pigmentation.^{233,234} PAM measurements show a pronounced photoinhibition during noon, from which the thalli recover when the UV stress decreases.¹⁰⁹ When exposed to high levels of solar UV-B radiation they produce UV-absorbing compounds, which seem to be hydroxycinnamic acid derivatives.²³⁵ Aquatic flowering plants are also affected by solar UV. Sea grass meadows cover large areas of sandy bottom in shallow water²³⁶ and contribute substantially to the aquatic biomass productivity.²³⁷ Photosynthetic quantum yield dramatically decreases under unfiltered solar radiation. Removal of UV-B or total UV improves the photosynthetic activity.²³⁸ Transfer experiments on plants growing at 15 m to 2.5 m water depth indicate an efficient adaptation of sea grasses to higher solar UV. Epiphytes growing on sea grass leaves has been considered detrimental since it reduces the photosynthetically available radiation, but as they strongly absorb UV-B radiation they exert a beneficial effect.²³⁹ In a submersed aquatic angiosperm, UV-B exposure over 7–16 days caused an increase in several photosynthetic enzymes. Water transparency to visible and UV governs the distribution and abundance of submerged macrophytes in lakes in the Canadian Arctic.²⁴⁰ Antioxidant enzymes were also activated by UV.²⁴¹ The common freshwater duckweed, *Lemna*, shows strong responses to simulated solar radiation, with a pronounced increase in ROS responses. This UV-induced stress response was augmented by

exposure to copper, which alone also activates the ROS pathway.²⁴² Related species differ considerably in their UV-B sensitivity.²⁴³

Consumers

Consumers form the next higher level in the aquatic food webs after producers (Fig. 3). In most cases several trophic levels follow each other, usually starting with zooplankton being the primary consumers. It is evident that a UV-related decrease in primary producer biomass has an effect on growth and survival of the consumers. In addition, specific UV effects have been identified in almost all consumers.²⁴⁴

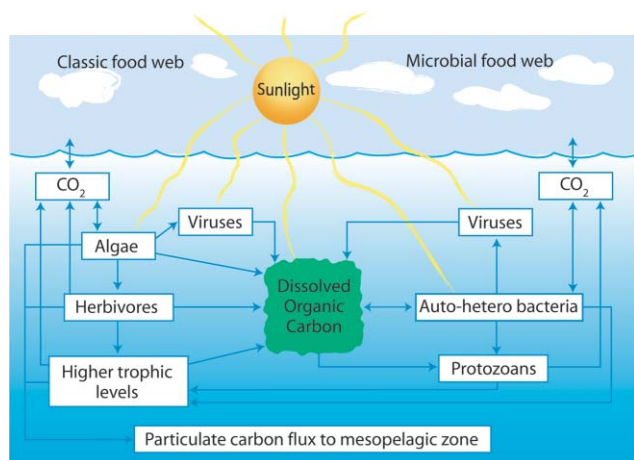


Fig. 3 Schematic diagram of classic and microbial marine food webs illustrating the flow of carbon and energy through the systems. Adapted from DeLong and Karl, courtesy of the National Biological Information Infrastructure (NBII).²⁴⁵

Zooplankton

Zooplankton includes unicellular and multicellular life forms and can be classified in several size classes. It is also comprised of larval forms of fish, crustaceans, echinoderms, molluscs and other phyla. These forms will be discussed below.

Zooplankton community structure in freshwater ecosystems is controlled by multiple factors, including DOC content and distribution throughout the water column, which regulates UV penetration (see ref. 2). UV radiation is a potential driving force for zooplankton community structure in some lakes.²⁴⁶ In shallow ponds of Finnish Lapland *Daphnia* only occurs when sufficient amounts of DOC are present.²⁴⁷ Depending on the terrestrial succession in the watersheds of several Alaskan lakes, the UV attenuation depths (1% of surface irradiance at 320 nm) vary from 0.6 m to more than 14 m. This UV regime strongly controls the species composition of major macrozooplankton. When zooplankton from a UV-opaque lake was transplanted into the surface water (0.5 m depth) of a UV-transparent lake, it perished within only a few days, suggesting a strong link between early succession of zooplankton communities and terrestrial plant communities (a source of DOC) within the watershed. Large variations in UV sensitivity were also found in a study involving lakes of different UV transparencies.^{248,249} In response to high solar UV, *Daphnia* shows a pronounced avoidance response when observed in UV transmitting acrylic columns suspended in the

surface waters. In contrast, when UV-B and short-wavelength UV-A are blocked, the animals prefer moving to the surface. In a low-UV lake, no such preferential behavior was seen. These results and those from a follow-up, open-lake experiment indicate that UV radiation may influence the vertical distribution and habitat partitioning of certain zooplankton in high-UV lakes, while predation, food availability and other factors may be more important in low-UV lakes.²⁵⁰ Studies of sublethal effects of UV on the freshwater cladoceran *Daphnia* show increases in respiration rates at low levels of UV exposure and decreases at high levels.²⁵¹

In their natural habitat, zooplankton face conflicting selection pressures. While invertebrate predators induce an upward movement during daylight hours, this exposes zooplankton to strong surface UV exposure.²⁵² Even though *Daphnia* and other zooplankton try to escape from surface UV radiation by vertical migration, the organisms cannot avoid excessive exposure. The copepod *Boeckella*, living in Lake Titicaca with very high solar UV levels, counters the detrimental effect by incorporating photo-protective MAAs.²⁵³ Copepods cannot synthesize these substances but acquire them from their algal diet (e.g., dinoflagellates).¹⁶⁰

In a study of Antarctic copepods, MAA concentration was strongly correlated with UV tolerance.²⁵⁴ In an alpine lake there was a strong seasonality in MAA concentrations in phytoplankton and copepods with more than three times higher concentrations in the summer than in the winter.²⁵⁵ Besides vertical migration and UV screening, copepods rely on photorepair of UV-B-induced DNA damage²⁵⁶ as shown in species from Patagonia, Argentina.²⁵⁷ Photoenzymatic repair contributes significantly towards UV-B tolerance in many cladocerans.²⁵⁸ Some Antarctic copepods possess a less efficient photorepair mechanism, which has been attributed to the low temperatures typical of Antarctic lakes.²⁵⁴ The implication is that at elevated temperatures (due to global warming) the enzymatic photorepair of UV-induced damage should be more efficient.²⁵⁹ This hypothesis was tested in living *Daphnia* by extracting DNA at various temperatures. UV-induced DNA damage increased with temperature, but the light-dependent enzymatic repair more than offset the effect and the net DNA damage significantly decreased with increasing temperature.²⁶⁰ This result was supported by a study of planktonic rotifers and crustaceans in Northern temperate lakes where UV had less detrimental effects on abundance and reproduction at higher temperatures.²⁶¹ However, one study found that mortality and DNA damage were as high as at low temperatures in freshwater ciliates, indicating that photolyase has an optimal temperature for its activity.²⁶² It is interesting to note that although elevated levels of solar UV induce mutations, there does not seem to be evolutionary selection toward UV protection in halophilic crustaceans.²⁶³ Feeding experiments indicate that UV-B pretreated phytoplankton species negatively affect the life history of *Daphnia*.²⁶⁴ Adults were smaller, and a smaller number of juveniles with lower fitness were produced under these conditions than in the controls, indicating that UV-B had a significant effect on food quality and impaired energy transfer to the next trophic level.^{265,266} The effect of climate warming on macro-zooplankton is subtle: Copepod populations were reduced in size but those of ostracods increased.²⁶⁷ In contrast predation by fish has a major effect on population composition and density.

Several workers have reported results consistent with the hypothesis that UV influences zooplankton community structure

and succession during early lake ontogeny. Engstrom and co-workers²⁶⁸ studied the chemical and biological trends during lake evolution in recently deglaciated terrain near Glacier Bay, Alaska. They demonstrated that dissolved organic carbon (DOC) concentrations increased with lake age. Williamson *et al.*,²⁶⁹ investigating changes in UV attenuation and macrozooplankton community structure in these same lakes, showed a strong dependence of UV radiation transparency on terrestrially derived DOC. They suggest a link between the development of terrestrial plant communities within these lake watersheds, changes in lake hydrology, and the early succession of zooplankton communities following deglaciation. These results suggest that UV radiation may be a more important factor than previously recognized in determining the distribution and abundance of zooplankton in lake ecosystems.

Corals and sea anemones

Recent accelerated catastrophic coral mortality has been linked with several environmental factors including bacterial and cyanobacterial infections,²⁷⁰ increasing temperatures,^{271–274} marine pollution²⁷⁵ and human destruction of coral reefs. Many corals rely on the photosynthetic activity of dinoflagellates (zooxanthellae).²⁷⁶ At temperatures exceeding a thermal threshold, corals are bleached. The underlying mechanism could be photoinhibition of photosynthesis in the zooxanthellae induced by the production of reactive oxygen species.^{277,278} However, recent results indicate that corals and their symbionts may be capable of adapting to higher temperatures.²⁷⁹ Like corals, giant clams harbor symbiotic zooxanthellae. Clams also suffered mass bleaching on several reefs of the Great Barrier Reef.²⁸⁰ Virus-like particles could also be associated with coral mortality.²⁸¹

When symbiotic algae are exposed to solar radiation the host is also subjected to damaging solar UV radiation. Some stony corals expand their tentacles upon exposure to photosynthetically active radiation and contract them when encountering excessive radiation.²⁸² As a counter-measure to enhanced solar UV the algae produce MAAs, some of which are also transferred to the host.²⁷⁶ Moreover, the host develops antioxidant defences to protect itself from the photosynthetically produced oxygen. Herbicides also affect corals by impairing the photosynthetic symbiotic zooxanthellae.²⁸³ Laboratory-kept colonies of the coral *Stylophora* maintained minimal amounts of MAAs, but the concentration of the UV-absorbing pigments increased rapidly upon exposure to broadband UV.²⁸⁴ Four MAAs, produced by the zooxanthella *Symbiodinium*, increased first, followed by six additional ones which were synthesized at the expense of the primary MAAs.

Sea anemones occur in several color phenotypes. At the coast of Discovery Bay, Jamaica, pink morphs are more abundant in the lagoon and in deeper areas, while green individuals are found in the forereef (seaward and downward from the reef crest) and in shallower areas. Genetic analysis revealed two distinct variants with different UV absorbance and UV acclimatization capacities.²⁸⁵ A comparison of sea anemones with dinoflagellates or green algae as symbionts or asymbiotic species showed that the MAAs mainly reflect phylogenetic differences among the anemones rather than the presence or kind of symbiont.²⁸⁶

Sea urchins

Exposure to UV radiation causes apoptosis (cell self-destruction) in developing sea urchin embryos.²⁸⁷ Embryos of three sea urchin species from different habitats ranging from the Gulf of Maine to the Antarctic indicated significant amounts of accumulated DNA damage in the form of cyclobutane pyrimidine dimers (CPD). Biological weighting functions for DNA damage indicated a high sensitivity for UV-A radiation, but the most sensitive species show an increased susceptibility to UV-B correlated with the lowest concentration of UV-absorbing compounds.²⁸⁸ Larvae and embryos of these species dwell within 5 m of the ocean surface. UV-induced damage in the different larval stages was clearly correlated with the absence of MAAs. The absence of UV-screening substances strongly decreased survival.²⁸⁹ Further, the observed delays in early cleavage and following development were closely related with UV-induced DNA damage. Reproduction in the circumpolar sea urchin *Sterechinus* occurs during austral spring when ozone concentrations during the past 25 years have declined by more than 50%. When the planktonic embryos were exposed in the top 1 m of the water column, nearly all exhibited DNA damage and 100% showed abnormal development.²⁹⁰ UV-B removal prevented DNA damage. At depths below 3 m hardly any abnormal development or DNA damage occurred. The threshold for DNA damage from ambient solar UV-B was $\leq 25 \text{ kJ m}^{-2}$ (inducing $\sim 17 \text{ CPDs mb}^{-1}$) and levels $> 80 \text{ kJ m}^{-2}$ precluded normal development.

The Antarctic sea ice has been thought to protect the benthic invertebrate fauna from solar UV-B radiation. However, recent investigations showed that short-wavelength UV-B (down to 304 nm) is transmitted through the austral spring annual ice of McMurdo Sound where it causes DNA damage and mortality during the early development in sea urchin embryos.²⁹¹ The degree of damage and mortality varies from year to year and depends on the thickness of the sea ice and on the total column ozone.

Amphibians

During the last decade amphibian populations have suffered widespread declines and even extinctions on a global scale.^{292,293} Many different factors, including habitat destruction^{294,295} and fragmentation,^{296–299} global climate change,^{300,301} acid precipitation,^{302,303} environmental pollution,^{304–307} including anthropogenic pesticides^{306,308} and fertilizers,³⁰⁹ parasites,³¹⁰ introduction of exotic competitors and predators,^{311–316} fungal diseases,^{317,318} and other pathogen outbreaks,^{319–321} interannual variability in precipitation, as well as climate change-induced reductions in water depth at oviposition sites, have been suggested as responsible for those global declines.^{322,323} Since the 1990s, malformations have been noted in many parts of the United States³²³ and in many other countries all over the globe.^{324,325}

Among other factors, solar UV-B radiation has been variously implicated as a possible contributing factor³²⁶ involved in malformation and mortality, especially during the embryonic development. However, there are two conflicting views on the involvement of UV-B in amphibian declines.^{327,328} In a controlled laboratory study, leopard frogs (*Rana pipiens*) were exposed to unfiltered solar radiation or radiation without UV-B or total UV.³²⁹ Unlike natural conditions, the larvae in the laboratory

could not avoid exposure. Full sunlight caused *ca.* 50% mortality in early larval development, while filtered solar radiation had no effect. There was a clear correlation between solar UV doses and hindlimb malformation. *In situ* studies in the natural amphibian habitat showed a considerable protection from solar UV radiation by DOC and vegetation shading, especially during the sensitive development during spring.³³⁰ When exposed to ambient solar radiation under controlled conditions and when natural shade and refuge were eliminated, embryos and larvae of several anuran species died.³³¹ A subsequent quantification of the outdoor UV exposure in Northern Minnesota and Wisconsin wetlands indicated that the risks for UV-induced malformations and mortality are low for both Northern leopard and mink frogs. The exposure of amphibian eggs and larvae to solar UV radiation strongly depends on the concentration of DOC in the water column.³³² One important factor is oviposition behavior: species which lay their eggs in UV-protected sites may be more sensitive to solar UV exposure than those which deposit their eggs at the water surface.³³³ Amphibian species with the highest physiological sensitivity to UV-B are those with the lowest field exposures as a function of the location of embryos and the UV-B attenuation properties of water at each site. These results also suggest that conclusions made about vulnerability of species to UV-B in the absence of information on field exposures may often be misleading.³³³

Red-legged frog embryos (*Rana aurora*) appear to be tolerant to current ambient levels of UV-B, but radiation even slightly exceeding the ambient levels is lethal.³³⁴ Although embryonic size is a complicated issue and small size at hatching can change very quickly after feeding, even at ambient levels, larvae exposed to UV-B as embryos tend to be smaller and less developed than non-exposed organisms. Amphibians use behavioral, physiological and molecular defences against solar UV-B damage, but species-specific sensitivities may cause changes in community structure due to persistent UV-B level increases,³³⁵ but because some species may be more successful than others, changes in species composition can result.³³⁵

Fishes

Although humans use about 8% of the productivity of the oceans, that fraction increases to more than 25% for upwelling areas and to 35% for temperate continental shelf systems. For about one-sixth of the world's population (primarily developing nations), the oceans provide at least 20% of their animal protein. Many of the fisheries that depend upon the oceanic primary productivity are unsustainable. Although the primary causes for a decline in fish populations are predation and poor food supply for larvae, overfishing, increased water temperature, pollution and disease, and/or exposure to increased UV-B radiation may contribute to that decline. The eggs and larvae of many fish are sensitive to UV-B exposure (Fig. 4). However, imprecisely defined habitat characteristics and the unknown effect of small increases in UV-B exposure on the naturally high mortality rates of fish larvae are major barriers to a more accurate assessment of effects of ozone depletion on marine fish populations.

Visual predators, including most fish, are necessarily exposed to damaging levels of solar UV radiation. Skin and ocular components can be damaged by UV,³³⁶ but large differences are



Fig. 4 Fish eggs and larvae are specifically prone to UV-B radiation. Salmon Alevin larva has grown around the remains of the yolk sac. In about 24 h it will be a fry without yolk sac (courtesy Uwe Kils).

found between different species.³³⁷ Coral reef fishes can adapt to the UV stress by incorporating UV-absorbing substances, which they acquire through their diet, into their eyes and epidermal slime.³³⁸ Exposure to solar radiation induced “suntanning” in red seabream. Histological, colorimetric and chemical assays showed that the sun-exposed fish had up to five times higher concentrations of melanin.³³⁹ In addition to direct effects, including damage to biological molecules such as DNA and proteins and the generation of reactive oxygen species, photoactivation of organic pollutants and photosensitization may be detrimental. The damaging effects on eggs and larval stages may be enhanced by polycyclic aromatic hydrocarbons (PAHs) such as retene, which is a pollutant from pulp and paper mills.³⁴⁰

In goldfish, embryos are prone to UV effects during early development³⁴¹ and produce CPDs under UV radiation. These are more efficiently repaired in the presence of light.³⁴² Solar UV radiation has been shown to induce DNA damage in the eggs and larvae of the Atlantic cod,²⁹⁶ where larvae were more sensitive than eggs. Artificial UV causes massive apoptosis in larval embryos of Japanese flounders.³⁴³ Studies addressing biological weighting functions indicated a strong sensitivity towards solar UV-B. CPD loads as low as 10 per megabase DNA resulted in approximately 10% mortality. Use of video taping and measurement of oxygen consumption showed sublethal effects of UV radiation in juvenile rainbow trout³⁴⁴ Under worst-case scenarios (60% ozone loss, sunny weather and low water turbulence), solar UV-B eliminated buoyancy and caused mortality within 1 or 2 days.

Fish spawning depth strongly correlates with UV exposure. *In-situ* incubation experiments have shown that in a highly UV

transparent lake 100% of yellow perch eggs (*Perca flavescens*) are killed before hatching when exposed to full solar UV.³⁴⁵ In this same lake 92% of eggs are spawned at depths greater than 3 m, while in a nearby lake with low UV transparency 76% of eggs were spawned at depths shallower than 1 m. It is not known whether the fish are able to detect and avoid the high UV at shallower depths in the high UV lake or whether this spawning pattern is due simply to differential survival. In either case, the deeper spawning depths place the eggs in colder water where it takes them much longer to hatch compared to eggs spawned in the warm surface waters. A similar phenomenon has been observed in bluegill larvae (*Lepomis macrochirus*) in a UV-transparent lake where in 19% of nests the estimated UV-induced mortality of larvae exceeds 25%. Most nests are exposed to relatively low UV levels because they are either located at deeper depths or under overhanging branches.³⁴⁶ In fish aquaculture, specific measures are introduced, such as installing UV sunscreens to avoid UV damage to larval fish in the usually shallow habitats.³⁴⁷

Other aquatic animals

Early life stages of marine organisms, particularly eggs and larvae, are vulnerable to solar UV-B radiation. Rocky shore molluscs show an increased mortality and retarded development upon UV exposure. These detrimental effects are synergistically enhanced in the presence of other stress factors such as high temperatures or salinity, pointing to strong underestimation of the ecological impacts of climate change by not accounting for the complex interactions among such environmental variables as temperature, salinity and oxygen availability.³⁴⁸ Desiccation enhances mortality and negatively affects development in encapsulated embryos of rocky shore gastropods.³⁴⁹

The amphipod *Amphitoe valida* has high concentrations of MAAs and consequently low mortality while the isopod *Idothea baltica* has low MAA concentrations and shows high mortality. However, the latter species deposits all available MAAs into the eggs and embryos conferring protection to the progeny.³⁵⁰

Conclusions and consequences

With the recognition of the importance of UV radiation effects on aquatic ecosystems, there has been a plethora of publications which show that solar UV can adversely affect aquatic organisms. These studies document substantial impact on individual species yet considerable uncertainty remains with respect to assessing effects on ecosystems. Several studies indicate that the impact of increased UV radiation would be relatively low when considering overall biomass response while often, in contrast, the response is quite marked when the abundance, distribution and effects on individual species are considered. Ecosystem response to climate variability involves both synergistic and antagonistic influences with respect to UV radiation-related effects on aquatic ecosystems and these influences significantly complicate comprehension and prediction at the ecosystem level. 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 oceanographic biogeochemical provinces than through direct effects. Decreases in primary production would result in

reduced sink capacity for atmospheric carbon dioxide, with its related effects on climate change.

The global decline of amphibian populations seems to be related to several complex, interacting causes. While one review clearly rejected any link between solar UV-B radiation and amphibian decline³²⁸ evidence from more than 50 peer-reviewed publications from around the world shows that dozens of amphibian species are affected by UV-B.³²⁷

A number of new studies have both confirmed and strengthened evidence that UV-B has an important influence on the community structure of various aquatic ecosystems. In lakes, phytoplankton abundance may vary by orders of magnitude depending upon future climate–DOM–UV interactions.²⁸ Also, lakes often show thermal stratification and as a consequence plankton communities show vertical distributions where the UV regime can strongly control species composition.²³⁷ Other evidence supports the hypothesis that UV influences zooplankton and community structure and succession during early lake ontogeny.²⁶⁹ Mesocosm studies, including both phytoplankton and their grazers, suggest that species composition and population structure may be more influenced by UV-B than overall algal biomass.¹⁸⁶ These results suggest that UV radiation may be a more important factor than previously recognized in determining community structure in aquatic systems.³⁵¹

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