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Solar radiation and the evolution of life

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Abstract

Life on earth can be dated back to some 3.8 billion years, and several lines of evidence suggest that the level of atmospheric oxygen was very low even 2.45 billion years ago, but then started to accumulate rapidly. However only for the past 500 million years has the atmosphere been "fully oxygenated", i.e. with an O_2-concentration close to the present 20 %, which coincides with the development of large and complex life forms. The sun emits short-wave ultraviolet radiation (UVR) that is potentially harmful to life. While the present atmosphere absorbs all UV-C (< 280 nm), also the present biota face harmful levels of UV-B (280 – 320 nm) and UV-A (320 – 400 nm). It has been assumed that the evolution of higher life forms was linked with the establishment of a stratospheric ozone layer and thus a screening of UVR. This may not necessarily have been the case since also methane-derived organic hazes, sulfur vapour or aldehydes could have UV-screening properties. It is nevertheless reasonable to assume that early life for periods may have been at the edge of "mutation meltdown" partly due to high levels of mutagenic UV. On the other hand, low levels of atmospheric O_2 would mean reduced likelihood of photo-oxidative damage. It is remarkably, however, that diversification of higher life during the "Cambrian explosion" coincided with establishment of a modern atmosphere, and that the subsequent colonization of land took place after the ozone layer was established. This presentation will discuss the development of early life in parallel with the development of an oxygenated atmosphere and changed levels of UVR, and also demonstrate how present life is evolutionary adapted to cope with UVR and thus reflects "the ghost of UV in the past". These adaptations allow organisms to tolerate fairly high levels of UV, but place a heavy toll on metabolism and productivity in terms of costs associated with synthesis of pigments, antioxidants, gene-repair mechanisms as well as metabolic and behavioural adaptations.

Introduction

Life on earth can be dated back to some 3.8 billion years, and the oldest remains of cyanobacteria with photosynthetic capacity did probably originate approximately 3.3 billion years ago. Several lines of geochemical and geological evidence suggest that the level of atmospheric oxygen was very low even 2.45 billion years ago, but then started to accumulate rapidly. However only for the past 500 million years has the atmosphere been “fully oxygenated”, i.e. with an O_2-concentration close to the present 20 %. The rise in O_2- coincides with the development of more complex life forms (1-3). Hence life by far predates the “modern”, oxygenated atmosphere, and had probably existed in some simple form for perhaps as much as 500 million years before fossil evidence suggest presence of the cyanobacteria and hence photosynthesis. These early organisms could be autotrophic life forms fuelled by hydrothermal vents and thus shielded from surface water radiation. The first phototrophs needed, however, to face the challenge of harvesting photons in the visible part of the spectrum (> 400 nm), but at the same time surviving the harmful UV radiation (UVR, < 400 nm). It has been generally believed that without an oxygenated atmosphere and hence an ozone layer of any significance, the earths´ surface would be a very inhostile place for life. Nevertheless, the very fact that the atmosphere gradually became richer in oxygen over a time span of nearly 2 billion years until it reached a quite remarkable stability from about 0.5 billion years ago till present, suggest a long period of evolutionary adaptations to cope with high levels of UV. A significant shielding from UVR did probably occur long before the Precambrian period. It has been suggested that already at an atmospheric level of O_2 of less than 1 % of present, there might have been a significant reduction of UVR, so that by the early Proterozoic, the DNA-damage rates might have dropped by two order of magnitudes within a few tens of millions of years (4). This may have protected phototrophs sufficiently to create a positive feedback with enhanced O_2-production.

At present, stratospheric ozone (O_3) screens off all UV-C (< 280 nm), a considerable portion of UV-B (280 – 320 nm), while less of UV-A (320 – 400 nm). Since potential, biological damage increases with decreasing wavelength (and increasing energy per photon), the ozone layer is crucial for terrestrial life as well as life in the photic zone of aquatic systems. The relationship between oxygen and UV radiation is subtle, however, since high oxygen also promote photodamage by free radicals. UVR also have positive effects, not only for vitamin D synthesis, but also by reducing potential attacks from virus, bacteria, parasites etc. Hence, even if an organism suffer from UVR-induced direct or indirect photodamage, it may be beneficial in relative terms if it harms pathogens, parasites or competitors even more. Given the benefits of an energy-harvesting system like photosynthesis, and the need for most other organisms to harvest directly from the photoautotrophs, there must have been a strong evolutionary race towards UVR tolerance.

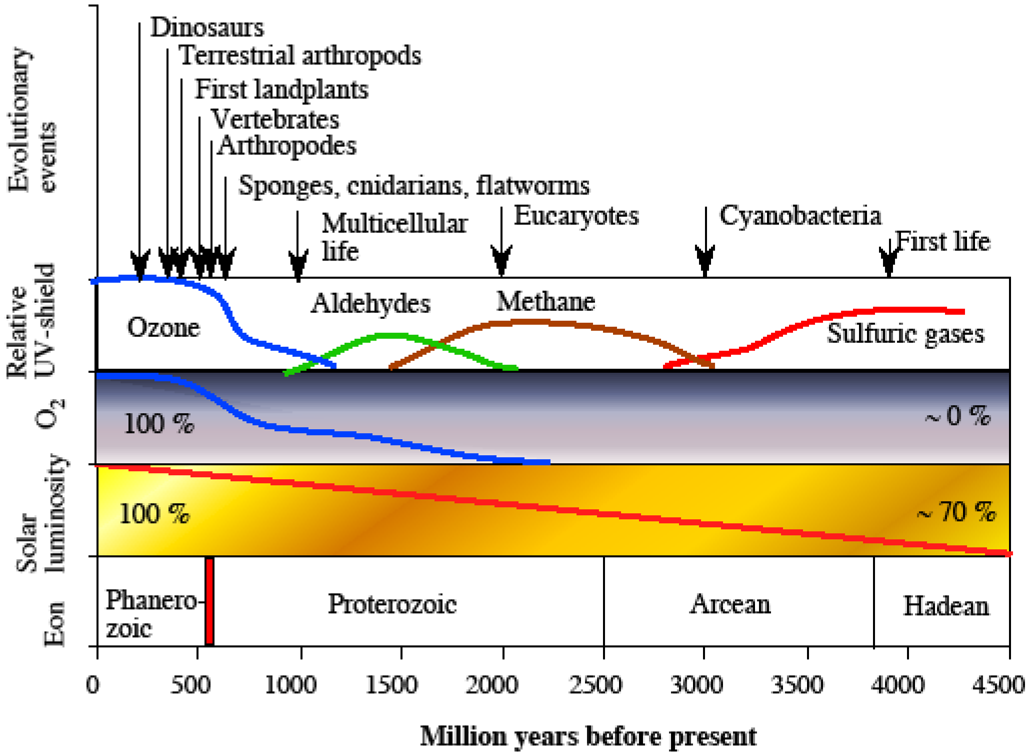

***Figure 1**. Conceptual graph illustrating some major milestones in the evolution of life related to potential presence of various UV-screening gases, the reconstructed level of atmospheric oxygen, the increase in solar luminosity and major periods (eons) of the history of Earth. Solid vertical line between the Proterozoic and the Phanerozoic indicated the fast diversification of metazoans called the Precambrian explosion.*

The Phaneroozoic era was initiated by comparatively large (centimetre to meter) soft-bodied animals which first appeared approximately 575 million years ago, and predated a sudden appearance of diverse metazoans with outer skeletons 25 million years later (5). This later and well-known “Cambrian explosion” resulted in a rapid speciation and radiation into a complex and diverse fauna some 550 million years ago. These events have been linked with the presence of atmospheric oxygen partly because it allowed for evolution of respiring organisms, and partly because it offered a sufficient shield against UVR for the very same fauna. Oxygen levels sufficient for respiration in metazoan do however predate the Cambrian explosion by at least 100 million years, perhaps more (cf. 3), and this have led some to question a direct, causal link from atmospheric O_2 to this remarkable evolutionary event. Margulis et al. (6) suggested that a series of physiological adaptation to cope with high UVR did evolve already before the onset of the Phaneroozoic era. Therefore the formation of an ozone layer may not necessarily be seen as a prerequisite for the evolutions of complex, shallow-water metazoans. Recent studies do however provide strong evidence of an anoxic deep ocean during the global Gaskiers glaciation, and that both oxygenated waters and appearance of large-bodies metazoans appeared shortly after the termination of this glaciation (5). These striking events in the history of life on Earth do very unlikely represent a pure coincidence, but the extent to which they can be linked to the establishment of stratospheric ozone and reduced UVR is not settled. A conceptual (and somewhat speculative) overview of the evolution of life related various factors in the history of Earth is provided in Fig. 1.

There is no doubt that there is a delicate balance between UVR as a promoter of evolution via high inducement of high mutation rates, and UVR as an obstacle to evolution due to *too high* mutation rates (“mutation meltdown”) (cf. 7, 8). The fast evolution of complex life and terrestrial life after the ozone layer was established do indeed suggest a deleterious effect of precambrian UVR. However, even with a fully oxygenated atmosphere for the past 500 million years, UVR has acted as a powerful, evolutionary driver partly as a highly mutagenic agent, partly by the needs to cope with this agent. I will here discuss the potential role of UVR for the evolution of precambrian life, and also discuss how present UVR acts as an evolutionary force which shapes life through a variety of behavioural and physiological adaptations.

Evolution of UVR on earths´ surface

The luminosity of the young sun was roughly 70 % of that of the present, but the spectral composition may have differed from the present one. It may be assumed, however, that UVR from the young sun was somewhat lower than today. The critical factors for biologically effects of UVR would be 1) presence of ozone, 2) other UVR absorbing gases, 3) UVR absorbing substances in aquatic systems 4) UVR-protecting properties of the biota itself and 5) dissolved O_2 and oxidative agents. By estimating oxygen deficits in the post-Gaskier oceans by the end of the Cambrian period, Canfield et al. (5) suggested that the atmosphere at that time must have had at least 15 % of present O_2-levels. Whether this would have been sufficient for a biologically relevant UVR-absorbance by ozone is uncertain. It was probably a transition phase where a build-up of ozone gradually became sufficient for evolution of complex metazoans. A period with high levels of non-ionizing radiation could have implied high evolutionary rates, certainly lots of malign mutations and failures, but also a fast radiation of body forms and species.

CO_2 do primarily absorb wavelengths < 190 nm and would thus not constitute any major UVR shield even in the early, CO_2-rich atmosphere, but there are other candidates for atmospheric UVR-absorption (9). Elemental sulfur vapour could be produced photochemically from volcanic SO_2 or H_2S, and sufficiently stable against photolysis to account for s significant UVR-screening in an anoxic atmosphere (9). S_8 absorbs over the entire UV range, while H_2S absorb mainly below 260 nm, and SO_2 above 260 nm. Hence a combination of these substances could offer a biologically relevant protection from UVR. It is also proposed that the late, Archean atmosphere was rich in biologically generated CH_4 and could have contained a hydrocarbon haze with UV-shielding properties (10). Sufficient accumulation of organic matter under aerobic conditions may have given rise to a vigorous methane production, yet the fate of this methane would also have depended on the presence of methanotrophs. Present emissions of CH_4 from aquatic systems and wetlands by methanogens is to a great extent regulated by methanotrophs, but periods with “mismatch” between production and consumption of CH_4 may have produced high atmospheric concentrations of CH_4 that both acted as a greenhouse gas as well as contributed to UV-absorbance. Finally a number of other organic compounds may for periods have had UV-screening effects in the atmosphere, not the least formaldehydes or aldehyde derivatives that may have produced by photolysis of other organic compounds.

For evolution of pre -terrestrial life, the UV-absorbance of water itself and aquatic, organic compounds or chromophores must have been vital. Pure water have rather high absorbance of UVR, and even in the most oligotrophic waters, the attenuation of UV-B generally implies a major absorbance of UV-B in the upper 10 m (11). Since photosynthetically active radiation (PAR) penetrates somewhat deeper than UVR, there might have been opportunities for photosynthetic activity in deeper layers. However early photoautotrophs must, like present aquatic plants, have faced the challenge of both harvesting PAR-light and coping with the harmful parts of the light spectrum. Productive waters, aas well as water with visual content of high-chromophoric dissolved organic carbon (DOC) such as humic compounds have an extremely high attenuation of shortwave light (11), see Fig. 2. Most likely both freshwaters and marine systems had very low levels of humus DOC, since there would be no allochthonous (terrestrial) source of humic matter. There might however have been periods of significant UV-absorbance from dissolved gases and inorganic substances. There is no conclusive information of spectral properties of lakes and oceans in the Archean (3800 – 2500 Ma) or the Proterozoic (2500 – 542 Ma). Under presence of chromophoric, dissolved compounds, the effect of ambient photo-products such as free radical and oxidants could, however, have profound effects on aquatic life.

It may be concluded that there probably have been periods with some UV-protection also for the Precambrian life, and probably a significant ozone layer had developed already in the Panerozoic: Still it is reasonable to assume that early life on earth experienced far higher UVR stress than present life.

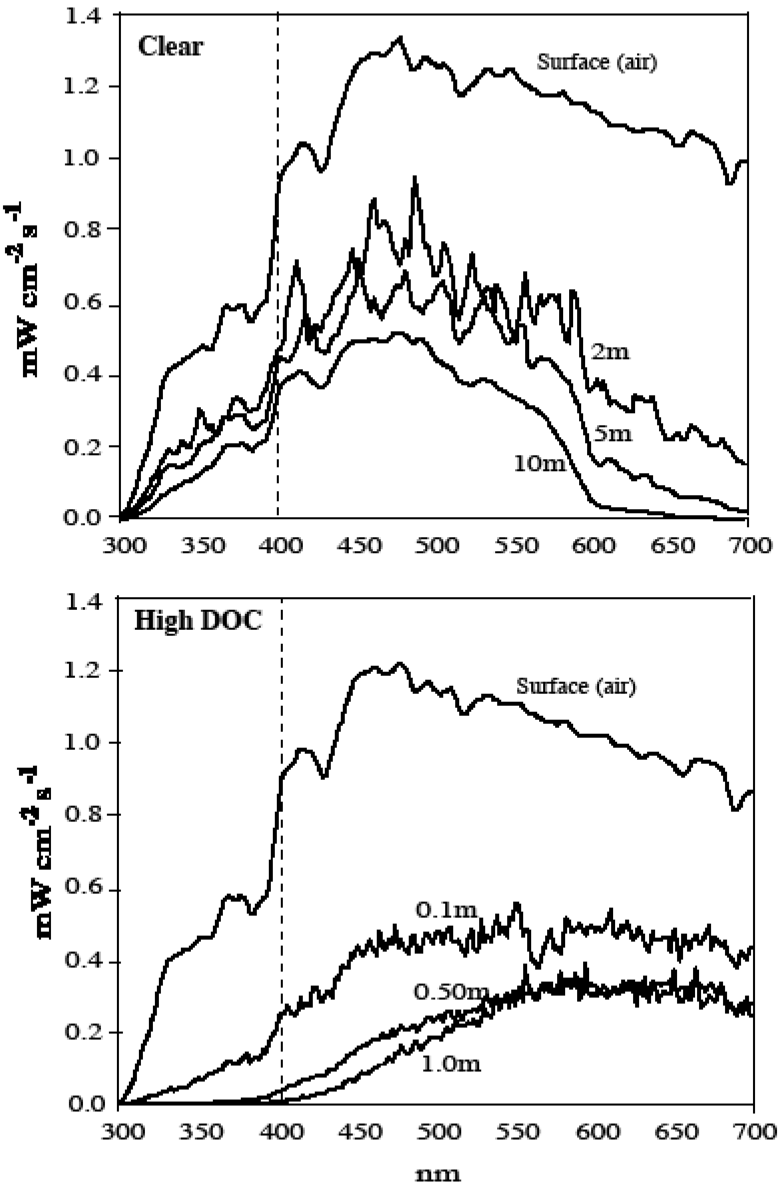

Figure 2. *Spectral profiles of a clear alpine lake (Bessvatn, Norway) and a forest lakes with higher levels of chromophoric dissolved organic carbon (DOC) (Skjervatjern, Norway). Irradiation at various depths indicated. UVR to the left of the broken vertical line. Even moderate levels of DOC may substantially increase the attenuation of short-wave light. Note that the intensities of UVR is far higher at 10 m depth in the clear lake compared with 10 cm in the DOC-rich lake (Mid-summer measurements at noon for both localities, LICOR 1200 Spectroradiometer, D.O. Hessen, unpublished data).*

Major events in the evolution of life

Late-Archaean rocks (2700 Myr) provide good evidence for presence of cyanobacteria (12), although photosynthesis may have predated the presence or these photoautotrophs. The origin of eucarytotes may also be of a similar age, yet most studies assume that eukaryotes are more recent, perhaps some 2000 Myr. Multicellular life like colonial algae and seaweeds were present from about 1000 Myr, while the first multicellular animals like sponges and cnidaria (jellyfish) were present from about 600 Myr. The first animals with a bilateral symmetry and an organized nervous system, the flatworms, also seem to have developed during this period. Slightly later, around 570 Myr, the first member of a highly successful group, the arthropods, occurred. These early arthropods were the ancestors of trilobites, crustaceans and insects.

The real diversification of life started with the onset of the Phanerozoic eon (542 Myr – present), where the “Cambrian explosion” (542 – 530 Myr) marked a striking diversification of multicellular life and larger animals with strong exoskeletons, like the trilobites. The first vertebrates, the jawless fishes, appeared at 505 Myr, and by 475 Myr, the first primitive plants had moved to land. These were vascular plants, however, and likely both green algae (the ancestors of vascular plants), terrestrial cyanobacteria and lichens had colonized moist land areas before this time. Presence of cyanobacterial mats on barren land in high arctic regions may give a hint on the adaptation of these terrestrial forerunners. Present mats of cyanobacteria is typically surrounded by an organic matrix and are also heavily pigmented, both of which offer a good protection from UVR for those with highest pigment levels (13). However, the colonization of land by higher plants and the first terrestrial arthropods (around 450 Myr) occupied land by the time when a significant UVR shielding by ozone probably was established. The first insects appeared around 400 Myr, by the time also the first terrestrial tetrapods developed from lobe-finned fishes.

UVR as an evolutionary force

The evolutionary responses to UVR include a wide range of behavioural, physiological and biochemical adaptations. This reflects the multitude of harmful effects that UVR has on cells. Membrane damage, often via lipid peroxidation, protein damage, production of free radicals and various types of DNA-damage may all put a heavy toll on sun-exposed organisms (14). Although action spectra with sufficient resolution have been provided for a very limited number of aquatic organisms (15, 16), they do all have the common property with rapidly increasing effects towards the lower end of the spectrum, and very limited effects in the PAR-area. Given the close biochemical make-up of all organisms, strong differences in action spectra should not be expected. For DNA damage, the relative biological response to wavelengths beyond 310 nm is negligible (17). Peak absorption for DNA is at 260 nm, and proteins have peak absorption around 280 nm, yet they both have “tails” into UV-B and UV-A. In an evolutionary context, mutations are the main agent by which UVR drive evolution. However, a major indirect evolutionary force of UVR is to counteract a deleterious mutation rate, given that the number of harmful mutation is likely to exceed the beneficial ones.

Evolutionary adaptations to cope with UVR

There are at least three major lines of defence towards harmful radiation; 1) behavioural mechanisms (migrations, nocturnal activity etc.), 2) screening or absorption (i.e. pigments like mycosporine-like amino acids, carotenoids or melanin) and 3) cellular mechanisms (such DNA-repair, anti-oxidants).

1) Behavioural adaptations is perhaps best studied in aquatic animals that have to harvest algae, but at the same time avoid harmful levels of UVR. *Vertical migration* has been seen in a number of aquatic organisms, from planktonic crustaceans to fish (18). The general ability to respond on short-wave light by downward migration is also seen in fish (19). When placed in the quartz cylinders with three replicate treatments of visible, visible plus UV-A, and visible plus UV-A and B, cod larvae distributed themselves evenly throughout the vertical extent of the cylinder (15 cm) under the visible and visible + UV-A treatments. In the treatments exposed to visible +UV-A and B larvae were consistently found at the bottom of the cylinders, particularly at peak solar intensity. This was observable even on the first few days of the treatments when mortality or morbidity was not a factor. Such UVR avoidance seem also for fish to rely on UV-A receptors that have been found in a variety of fish species (20, 16), yet as for crustacean invertebrates also fish seem incapable of UV-B detection.

2) The conspicuous presence of pigmentation in light-exposed animals clearly provides these with a higher UVR tolerance (for a review, see 18). In fact the very presence of these UV-protective properties strongly suggests that UV is a potential stress factors, since all protective means have their cost. This is clearly seen as a general decrease in pigmentation with increasing depths, reaching the extreme in deep-water or cave-dwelling animals that may be almost completely devoid of skin pigmentation. Organisms like zooplankton, being susceptible to visual predators, face a dual challenge. Strong pigmentation implies high visibility and thus a high risk of predation. Lack of pigmentation, on the other hand, could render the animals more susceptible to UVR damage. In aquatic systems, predator-free, light exposed localities are generally inhabited by strongly pigmented, surface-dwelling species, while pigmentation decrease with

presence of visual predators. Melanins are highly complex macromolecules that serve as highly efficient screens for short wave radiation. They are widespread in all groups of metazoans, and have at least two key ecological functions: camouflage and UV-protection. The potential role of melanin in UV-protection is perhaps best illustrated by freshwater zooplankton. Some cladocerans have developed a highly conspicuous carapace melanization that appears to be a unique adaptation to UVR. Highly UV-exposed populations of various species and clones of the *Daphnia pulex* complex and *Daphnia longispina* may frequently have a dark appearance that most often is caused by a carapace melanization (21, 22). Melanin is quite widespread as UVR protective pigments in most animal phyla. A heterogenous category of UV-screening compounds is collectively labelled *Mycosporine-like amino acids* (MAA´s). These are widespread in shallow water organisms (23) absorb radiation primary in the 310-360 nm range and seem to be primarily associated with UV-stress. Probably most of the MAA´s in heterotrophs are derived via food from autotrophs (24). Finally Carotenoids may serve a dual role in photoprotection in organisms, serving both as an anti-oxidant or radical scavenger, and offering a protection from direct photon flux by quenching. The conspicuous red coloration of alpine and highly light exposed plankton is a typical evolutionary adaptation to cope with high UVR.

3) A third defence mechanism are intracellular processes such as repair of DNA damage and the production of quenching agents and anti oxidant enzymes that neutralize reactive oxygen species (ROS) produced by UV. Examples include carotenoids, involved in quenching of activated photosensitizers and singlet oxygen (25), superoxide dismutase, which eliminates the superoxide radical, catalase which detoxifies hydrogen peroxide and glutathione transferase which neutralize peroxidized macromolecules and detoxify breakdown products after lipid peroxidations (26). Antioxidants are linked with resistance against UVR in plants, microorganisms and mammalian cells and skin tissue (27, 28). A last major defence would be the various means of enzymatic photorepair that is probably a common property of all organisms. These general effects on DNA, proteins and membranes and the corresponding cellular repair mechanisms will not be reiterated here. It has for long been known that longer wavelengths, notably in the UV-A and blue, can counteract UVR damage by repair of DNA.

UVR and the evolution of sex and polyploidy

There are also some more general evolutionary changes that could serve as indirect means to cope with UV-induced damage. This could involve the evolution of sex and chromosome duplication, both mechanisms could provide genetic backups for allelic mutations. There are at least two major, evolutionary aspects that is worth mentioning. One is the link between solar induced radical damage and O_2-levels. Clearly the shift to a respiratory metabolism and increased extra- and intracellular levels of O_2 would have strongly promoted both DNA and membrane damage. Hence while the early life, including aerobic phototrophs, probably was exposed to higher levels of UVR, the low levels of O_2 induced less radical damage than that of precambric life. Evolutionary relevant mutation rates would also have depended on the ratio of introns to exons. A high fraction of introns (non-coding regions) could buffer against UV-induced damage. The intron:exon ratio vary tremendously, even within closely related organisms, but it is not known how this ratio has changed during the evolution of life.

Mechanisms that could provide genetic back-ups would most likely be promoted by UV-stress. While deleterious mutations could be fatal in asexual and clonal organisms, recombination would provide alternative alleles. Hence the evolution of sex could very well be based on this endogenously (cf. 29) way of fixing DNA-damage. The widespread occurrence of sexual reproduction - despite lower population increase in sexual organisms compared with the asexual alternative - still is an evolutionary puzzle. While beneficial in a long-term perspective by providing genetic variability at the population level, sexual reproduction would be a competitively inferior strategy in the short term. In an isolated, asexual population, malign mutations will accumulate, since there is no way of replaced mutated genes with the “wild-type”. This principle, known as Mullers´ rachet, would eventually put the whole population at risk. Since UVR will speed up the mutation rate, it could also have been a promoter of sex in various organisms (30).

Following the same line of reasoning, polyploidy (chromosomal duplication) could also be promoted by UVR. There is a striking increase in the incidence of asexual reproduction as well as polyploidy towards harsh climates such as alpine areas and notably the Arctic. This has clearly been verified for terrestrial plants (30) and also for invertebrates (31) as well as freshwater fish (32). Polyploidy is thought to be important for maintenance of genetic diversity in the absence of sexual reproduction and could also enhance expression of genes, and through polyploidization, reproductive isolation (i.e., new species) may arise in a single or few generations. The fact that many organisms seem to be particularly vulnerable to UV-stress in the Arctic (18 and papers herein) could be one alternative explanation to the high incidence of chromosome duplication in cold and harsh climate.

UVR as a negative or positive evolutionary force?

UVR is generally seen as a having a strong impact on life due its strong mutagenic effects and its potential for promoting oxidative damage on membranes or proteins. There is clearly a trade-off, however, where a high mutation load may have prevented evolution of higher life forms and terrestrial life for long periods, at moderate levels it may also have promoted a rapid microevolution and diversification. Hence for life as such, rather than for the individual organisms, UVR might in general have acted as a positive evolutionary force, at least since the Precambrian period.

There are, however, other means by which UVR could act as a positive force for organisms. To the extent that pathogens such as viruses, bacteria and other parasites are more negative impacted by UVR than their host or target organism, the host may actually benefit from UV-exposure. Also if competitors or predators suffer comparatively more from UVR than other community members within the ecosystem, this could yield an *apparent* positive effect of UVR on prey or competitor species (33).

Also animals may depend on UVR for D-vitamin synthesis in the skin. It has been suggested that photoproduction of vitamin D in the skin was essential for the evolution of terrestrial vertebrates; the strong skeleton needed for quadripodes on land could probably not have been supported in the poikilotherms without solar aid for converting previtamin D_3 to vitamin D_3 (34). In fact the prevalent habit of seeking direct solar exposure also for many present day terrestrial poikilotherms may not only serve for a general “warming up”, but could also serve the important role of supporting vitamin D synthesis.

Conclusion: the ghost of past UVR

Life is adapted to cope with UVR, and thus minor changes in UV exposure are unlikely to have dramatic impacts. Organisms which did not evolve sufficient mechanisms to cope with UVR are long gone. This is not to say that UVR is presently without costs. On the contrary, there are numerous examples that productivity increases when organisms are released from UVR. Typically organisms immediately slow down their synthesis of photoprotective compounds in the absence of short-wave radiation. From an evolutionary point of view, it would be expected that all sorts of metabolically expensive mechanisms are inducible and flexible and thus can be adjusted to optimal levels. E.g. UVR exposed populations of *Daphnia* that are strongly melanized, survive far better under solar exposure than their hyaline counterparts. They are, however, competitively inferior at low levels of UVR due to the costs of synthesizing melanin after each molt (22), which in the absence of UVR are shut down.

Based on the assumption that early life has experienced far higher levels of UVR than that at present, it is likely to assume that the capacity for inducible defences is widespread. Especially phototrophic organisms are remarkably efficient in protecting vital compounds from UV-induced damage, even if the overall production is impaired. Typically, surface dwelling phytoplankton species are rich in polyunsaturated fatty acids (PUFAs) during the spring bloom, and these are of vital importance for the entire marine food web. However in contrast to PUFAs in a non-living context (e.g. fish-oil) that undergo fast oxidation of double bonds and hence becomes rancid in the presence of light and oxygen, live phytoplankton cells seem to have a substantial capacity to protect their PUFAs even under high levels of UVR, even if the C-fixation and production may be strongly impaired by the same levels of UVR (35).

Present life is the result of a continuous, yet variable, selection since the onset of life at Earth. Most likely UVR has been, and still is, one of the major ambient selective pressures. Hence present life reflects “the ghost of past UVR”, to paraphrase the common ecological saying that present ecosystem communities reflect the ghost of competition in the past.

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