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REVIEW ARTICLE

Harmful effects of UV radiation in Algae and aquatic macrophytes – A review

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Abstract

This study provides an overview of the available literature on the ultraviolet-B (UV-B – λ=280-315 nm) and UV-A radiation (λ=315-400 nm) effects on algae (micro and macroalgae) and aquatic macrophytes, like seagrasses and liverworts. It includes studies on prokariotic cyanobacteria, haptophytes, diatoms, dinoflagellates, red algae, brown algae and chlorophytes from freshwater (ponds, lakes) to marine littoral and Open Ocean. It also reports available studies concerning on marine and freshwater plants exposed under UV irradiation. Since the reported relationship between the human activity and the depletion of the protecting layer, the effects of ultraviolet radiation in the biological relevant wavebands on algae and on organisms in general have become an important issue over the past three decades and will be also important in the next few decades. Virtually, all aquatic organisms depend on algae and aquatic plants (submerged or near shallow line) for food, shelter, also as oxygen supplement and CO2 sequestration by photosynthetic procedure. This review reports on harmfull effects caused by ultraviolet wavebands on photosynthetic organisms in their natural habitats.

Key words: Algae, cyanobacteria, Macrophytes, UV-radiation

Introduction

Aquatic systems (freshwater, marine or brackiswater) cover about 71% of the Earth's surface, being the hydrosphere. Aquatic photosynthetic organisms are the main support of the entire life of these systems, ranging from cyanobacteria, algae, to aquatic angiosperms.

Algae are an extensive group of photosynthetic organisms distributed through a wide variety of habitats. It is a group beyond the taxonomy, as it includes several taxonomic kingdoms. Algae occur in freshwater ponds, shores and coasts attached to the bottom by more or less complex fixations of the thallus (benthic species) or live suspended in the water column, being the phytoplankton. It can be found also in the open ocean, from intertidal shores to a depth of 150 metres. There are also terrestrial forms, on soils and among bryophytes. According to individual size, and cell organization, algae can be divided into two categories: microalgae (great number of photosynthetic unicellular organisms being the smallest ones the cyanobacteria) and macroalgae (multicellular organisms characterized by a body named thallus, with no differentiation in roots, stems and leaves, although in kelp a great complexity in thallus structure can be found). Altogether, the algae probably account for more than half the world total primary production (Hoeck et al., 1995). This group is characterized by a great diversity of sizes, forms, body structure, distribution and ways of life. Virtually, all aquatic organisms depend on their production for food, shelter and oxygen supplement. They also perform CO_2 sequestration by photosynthetic procedure and play a role as pH regulators. Algae are extremely important not only ecologically but also phylogenetically (Hoeck et al., 1995) because understanding the diversity and the phylogeny of the plants relies on algae research (Hoeck et al., 1995). There is an agreement by the scientific community that life originated in the sea and that many ancient evolutionary lineages can be found there (Hoeck et al., 1995).

The interest in commercial utilization of algae (Spolaore et al., 2006; Cardozo et al., 2007; Stengel et al., 2011) or specifically of cyanobacterial secondary metabolites (Rastogi and Sinha, 2009) is another challenge and is increasing recently based

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on different fields of science (nutrition, environment, medicine, pharmacology). Many of their valuable chemical constituents exhibit multitude bioactivities with applications in the food, as pigments source, cosmetic, new natural sunscreens (Coba et al., 2009), pharmacological (Thomas and Kim, 2011), agri- and horticultural sectors, in human health (Stengel et al., 2011), carrageenans extraction (Campo et al., 2009), and in biofuels production (Chisty, 2007). Cyanobacteria, like *Anabaena* or *Nostoc* are also well documented as natural soil biofertilizerers in rice fields (Banerjee and Häder, 1996; Sinha et al., 1998, 2002).

Since publication of the 1998 UNEP Assessment, there has been continued rapid expansion of the literature on UV-B radiation, and many measurements have demonstrated the inverse relationship between column ozone amount and UV radiation (McKenzie et al., 2003), from around 1970 (20^{th} century) until the end of the 20^{th} century (Björn, 2007). There is almost complete consensus regarding the major cause of this: anthropogenic pollution of the atmosphere (Björn, 2007) due to a rapid industrialization in the past few decades related to an increase pollutants such as chlorofluorocarbons (CFCs), halocarbons, chlorocarbons (CCs), organobromides (OBS), carbon dioxide (CO_2), methyl chloroform (MCF) and dioxins (NO_x) that are responsible for the depletion of the UV-screening ozone layer in the stratosphere (references in Singh et al., 2010). The most dramatic expression of this is the Antarctic ozone hole (Björn, 2007). At northern mid-latitudes, the 1997-2000 ozone losses were around 6% relative to 1980 levels, which might result in a UV-B increase of up to 12% (McKenzie et al., 2003) as referred by Arróniz-Crespo et al. (2008). Decreased ozone levels are expected to recover to pre-1970 levels by 2050 (McKenzie et al., 2003). So, ultraviolet radiation, especially its effects on terrestrial and aquatic living organisms, became an important issue over the past three decades and will be also important in the years to come.

Artificial UV-B (λ=280-315 nm) radiation may be used as disinfectant preventing toxic algal blooms (or pathogens) on potable water (Alam et al., 2001), unfiltered surface water (Cantwell and Hofmann, 2008), lakes (Sakai et al., 2007b), wastewater treatment (Blatchley et al., 1997; Mamane et al., 2010) and ballast waters, killing potential invasive living organisms (Martínez et al., 2012). UV-C (λ=200-280 nm) radiation may be a tool to eradicate algae in caves (Borderie et al., 2011).

There are several important reviews on harmful effects of UV radiation on aquatic ecosystems: aquatic ecosystems in general (Häder et al., 1998; Häder, 2000; Hood et al., 2006); marine plankton (Davidson, 1998); marine organisms in Antarctic region (Karentz and Bosch, 2001); algae (Holzinger and Lütz, 2006); plant cells (Kovács and Keresztes, 2002); spore germination in algae (Agrawal, 2009); cyanobacteria (Sinha and Häder, 2008; Singh et al., 2010); cyanobacteria, phytoplankton and macroalgae (Sinha et al., 1998); cryptogams - cyanobacteria, algae, lichens, mosses, liverworts, pteridophytes and fungi - (Björn, 2007); macroalgae (Poll, 2003 referred by Björn, 2007); rhodophytes (Talarico and Maranzana, 2000); freshwater rhodophytes (Necchi Jr, 2005); seagrasses (Short and Neckles, 1999); corals and coral bleaching (Baker et al., 2008; Tambutté et al., 2011); molecular effects (Jenkins et al., 1995; Glatz et al., 1999); methods for DNA damage detection (Sinha and Häder, 2002); genetics (Xiong et al., 2009); cyanotoxin nodularin production (Pattanaik et al., 2010); lipids and lipid metabolism (Guschima and Harwood, 2006); lake acidification and UV penetration (references in Häder et al., 1998); carbon flux and ecosystem feedback (Wassmann et al., 2008) and ecological and environmental impact (Häder and Sinha, 2005; Carreto and Carignan, 2011). The present review concerns the major general effects that UV radiation causes to aquatic photosynthetic organisms, updating previous reviews.

Algae and UV radiation – harmful effects

Aquatic systems with high transparency of oligotrophic waters (marine and freshwaters) are exposed to the highest levels of ultraviolet radiation. Intertidal and epipelagic marine living forms also face the same situation especially those that can't move away in high light periods, like benthic macroalgae, seagrasses and other macrophytes. UV irradiation in lakes can affect photosynthesis of plankton organisms down to a depth of 10-15 m (Holzinger and Lütz, 2006). In marine waters, UV-B can penetrate down to a water depth of 20-30 m (Smith et al., 1992 referred by Dahms and Lee, 2010) and in clear Antarctic Ocean it may reach depths of 70 m (reference in Short and Neckles, 1999). In clear Antarctic oceanic waters UV-A can penetrate to a depth of between 40 and 60 m (Ban et al., 2007 referred by Dams and Lee, 2010), depending, among others, on the incidence of solar radiation, transparency of waters and wind mixed layer effects.

Tidal exposure also imposes considerable environmental stress on intertidal seaweeds such as elevated irradiance levels, temperature changes and desiccation, especially in spring low tides, which occur every month during new and full moon phases. Typically, seaweeds sensitive or intolerant to ambient stresses inhabit the lowermost intertidal zone (where emersion at low tide is brief and/or absent), while those found at higher elevations usually possess heightened tolerance to environmental fluctuations (Sampath-Wiley et al., 2008). Since UV radiation daily doses in the intertidal system are much higher than in the sublittoral zone, there is a relashionship between UV radiation tolerance and vertical distribution of intertidal macroalgae (Altamirano et al., 2003).

There are numerous studies relating harmful UV effects of radiation with decreased performances or death of the target organisms. As regard algae and aquatic plants, these studies especially concern UV-B wavebands effects on growth and development (Banaszak and Trench, 1995a; Braune and Döhler, 1996; Grobe and Murphy, 1997, 1998; Häder et al., 1998; Makarov, 1999; Cordi et al., 2001; Estevez et al., 2001; Altamirano et al., 2003; Altamirano et al., 2004; Huovinen et al., 2006; Andreasson and Wängberg, 2007; Zeeshan and Prasad, 2009; Dahms and Lee, 2010; Dahms et al., 2011), biomass, productivity and photosynthesis (Helbling et al., 2008; Sampath-Wiley et al., 2008; Zeeshan and Prasad, 2009), buoyancy (Ma and Gao, 2009), sensitivity (Banerjee and Häder, 1996; Zudaire and Roy, 2001; Marshall and Newmann, 2002; Arróniz-Crespo et al., 2008), photosynthetic pigments (Döhler and Buchmann, 1995; Döhler and Lohmann, 1995; Aráoz et al., 1998; Bhargava et al., 2005; Huovinen et al., 2006; Sampath-Wiley et al., 2008; Heo and Jeon, 2009), reactive oxygen species (Mallick and Mohn, 2000; Downs et al., 2002; He and Häder, 2002; Rastogi et al., 2011), antioxidant system (Estevez et al., 2001; Dummermuth et al., 2003, Bolige et al., 2005; Barros et al., 2006; Janknegt et al., 2007; Wang et al., 2007; Sampath-Wiley et al., 2008; Wang et al., 2008; Delgado-Molina et al., 2009; Lee and Shiu, 2009; Mogedas et al., 2009; Ryu et al., 2009; Tian and Yu, 2009; Pallela et al., 2010; Zeeshan and Prasad, 2009; Dahms and Lee, 2010; Li et al., 2010; Hupel et al., 2011, Liu et al., 2011), protein (Sass et al., 1997) and DNA damage (Buma et al., 2001; Kumar et al., 2004; Sakai et al., 2007a; Rastogi et al., 2011), nutrition quality (Leu et al., 2006; Nahon et al., 2010), lipid/fatty acid content (Skerrat et al., 1998; Khotimchenko and Yakovleva, 2005; Liang et al., 2006) enzyme activity (Lee and Shiu, 2009), C:N:P fixation (Hessen et al., 2008) and nitrogen assimilation (Döhler and Buchmann, 1995; Döhler et al., 1995; Babin et al., 1996; Braune and Döhler, 1996; Döhler, 1997, 1998; Wängberg et al., 1998; Xu and Gao, 2012), nutrient cycling (Anusha and Asaeda, 2008), P uptake (Hessen et al., 2012), system ecology (Carreto and Carignan, 2011), and synergistic effects under xenobiotics presence enhancing toxicity on target organisms (Barron and Ka'Aihue, 2001; Bhattacharyya et al., 2011).

Algae (and the organisms in general) may develop a wide strategies to cope with UV radiation like vertical migration, multiple layered cell walls, absorbing screening compounds such as carotenoids, mycosporine-like amino acids (MAAs), scytonemines (only cyanobacteria) (Banaszak and Trench, 1995b; Sinha et al., 1998; Klisch and Häder, 2008; Singh et al., 2010), protective mechanisms (e.g. Malanga et al., 1999; Marshall and Newman, 2002; Carreto and Carignan, 2011; Hupel et al., 2011), proteins and some repairing enzymes, that enable adaptation to environmental stress (Marshall and Newman, 2002; Hanelt and Roleda, 2009).

Besides the large amount of work on this subject, many of them were made under conditions with supplemental UV-B irradiance higher than would ever occur in nature (Xue et al., 2005). Most of the studies on the action of UV radiation on species cultures involve short duration photosynthesis experiments. Such studies have limited value for understanding UV-resistance in the field or adaptation of the whole organism (Holzinger and Lütz, 2006). Recent studies are conducted under experimental conditions and supplemental UV-B irradiance that tend to approach realistic UV- radiation conditions existing on Earth's surface. Some are related with a wide range of deleterious effects of UV-irradiation also describing survival mechanisms under high levels of UV-B and other environmental parameters.

The effects of UV radiation on organisms in natural conditions are complex because synergy is involved on deleterious and recovering mechanisms to face UV irradiation. The susceptibility to elevated UV-B radiation is dictated by a complex interplay between protection, repair and other factors that may lead to highly variable UV-B susceptibility among the species (Zeeshan and Prasad, 2009).

Wavebands of UV radiation: differential effects on algae

The term UV radiation (UVR) describes the UV region from 280 to 400 nm. UVR is usually divided into three spectral regions: UV-C (λmax = 200 to 280 nm), UV-B (λmax = 280 to 315 nm) and UV-A (λmax = 315 to 400 nm). Studies related with the effects of UV radiation, usually concern wavebands from 280 to 400 nm (UV-A+UV-B), compared with PAR. PAR is an abbreviation of photosynthetic active radiation, which is the spectral range of solar radiation from 400 to 700 nanometres that enables photosynthesis process by photosynthetical organisms.

The wavebands of UV radiation (UV-C, UV-B and UV-A) act differently on algae. Their modes of action are also different in other organisms, but they will not be referred here. Short UV-B wavelengths result in a higher degree of DNA damage, higher levels of oxidative stress, and greater expression of cell cycle genes, than exposure to UV-A, therefore promoting apoptosis (reference in Dahms and Lee, 2010) because longer UV-A wavebands are closer to PAR.

UV-A generally causes indirect DNA damage by the formation of chemical intermediates such as oxygen and hydroxyl radicals that interact with DNA to form strand breaks, DNA-protein cross-links and alkali labile sites (reference in Dahms and Lee, 2010). On the other hand, UV-B causes direct DNA damage by inducing the formation of cyclobutane pyrimidine dimers (CPDs) and pyrimidine-pyrimidone (6-4) photoproducts (Dahms and Lee, 2010). These products can cause mutations or have cytotoxic effects by inhibiting replication or the expression of essential genes (reference in Dahms and Lee, 2010).

UV-A is a powerful prooxidant, inducing both strand breaks and alkali labile sites (Pfeiffer et al., 2005 referred by Dahms and Lee, 2010), whereas UV-B produces mainly CPDs.

However, moderate levels of UV-A may stimulate photosynthesis and growth in both micro and macroalgae (references in Xu and Gao, 2010). *Gracilaria lemaneiformis* (Rhodophyta) shows an increase relative growth rate in the presence of UV-A, while UV-B inhibited it (Xu and Gao, 2010). The positive effect of UV-A counteracted negative effect of UV-B, resulting in an insignificant impact of UVR on growth (Xu and Gao, 2010) of this alga. Xu and Gao (2010) study, showed that during the noon period, both UV-A and UV-B resulted in the decrease of maximum quantum yield (F_v/F_m), but UV-B aided in the recovery of the yield in the late afternoon, reflecting that UV-B might be used as a signal in photorepair processes.

UV-C is the most damaging range of the spectrum (Banaszak and Trench, 2001) but it is not of biological relevance because it is totally absorbed by the atmosphere (Banaszak and Trench, 2001; Holzinger and Lütz, 2006; Basti et al., 2009).

Few studies have been carried out on the UV-C effect on established algal colonies. Borderie et al. (2011) showed that after various periods of UV-C exposure, the photosynthetic activity of algae was strongly decreased and even annihilated, which could be related to a degradation of their photosynthetic apparatus and pigment contents. After UV-C exposure, algal cells reinoculated on fresh medium were unable to proliferate (Borderie et al., 2011). UV-C radiation generates oxidative stress and genotoxicity effects. It is also known (Borderie et al., 2011) to induce programmed cell death (PCD) by a production of cyclobutane-pyrimidine dimers and DNA photoproducts, which are involved in cellular lethality, senescence and mutagenesis (references in Bordrerie et al., 2011).

Oxidative stress

Environmental stresses (high light, nutrient deficiency, drought, heavy metals, high salt concentration, extremes of temperature, UV radiation, air pollutants, water stress, herbicides, mechanical and physical stress) induce the production of reactive oxygen species (ROS) (Dummermuth, et al., 2003). ROS are always formed by the inevitable leakage of electrons onto molecular oxygen from the electron transport activities of chloroplasts, mitochondria and the plasma membrane (Mallick and Mohm, 2000). Reactive forms of oxygen include the superoxide radicals (O^{-}_{2}), singlet oxygen ($O^{\square}$) the hydroxyl radical ($OH^{\square}$) and hydrogen peroxide (H_2O_2). All these can react with certain biomolecules, altering or hampering their biochemical activities. The combined biological effect of these toxic oxygen species on organisms is termed "oxidative stress" (Mallick and Mohm, 2000).

Studies with the cyanobacterium *Arthrospira (Spirulina) platensis* by Ma and Gao (2010) show that associated accumulation of reactive oxygen species and presence of UVR resulted in the spiral breakage by oxidizing the lipids of sheath or cell membrane.

Rhodophytes like *Gelidium amansii* (Lee and Shiu, 2009) or *Corallina officinalis* (Li et al., 2010) are two examples of production of free H_2O_2 to seawater and lipid peroxidation induction when exposed to UV-B radiation. Hydrogen peroxide

itself is not particularly reactive with most biologically important molecules, but it is probably an intracellular precursor for more reactive oxidants as it passes quickly through membranes by diffusion (Apostol et al., 1989 referred by Dummermuth et al., 2003). If accumulation of ROS exceeds the capacity of enzymatic and non-enzymatic antioxidant systems, the photosynthetic apparatus is damaged due to destruction of lipids, proteins and nucleic acids, finally leading to cell death (Estevez et al., 2001; Dummermut et al., 2003). Under physiological conditions of growth, oxidative stress associated to development leads to a significant decrease on cellular antioxidant capacity (Estevez et al., 2001).

Dummermuth et al. (2003) study shows that the measurement of the in vivo fluorescence of photosystem II is a suitable tool to determine the effect of oxidative stress on macroalgae.

Growth and development

The negative effects on growth and development caused by UV-B irradiation is well documented, and usually relative growth rates (RGR) are also related to UV damage to the photosynthetic machinery, photosynthetic pigments, antioxidant enzymes and lipid peroxidation caused by increasing UV radiation.

The green macroalga *Ulva expansa* (Setch.) S. and G. grown in an indoor tank under controlled photoperiod and UV-B levels showed significantly lower growth rates on algae segments exposed to the unscreened UV-B lamps as compared to UVO-screened lamps (Grobe and Murphy, 1997). Makarov (1999) reached the same conclusion regarding the influence of UV radiation on growth rate of nine species of macroalga: Phaeophyta (*Laminaria saccharina, Alaria esculenta, Saccorhiza dermatodea, Fucus distichus, Fucus serratus, Fucus vesiculosus*), Rhodophyta (*Palmaria palmata, Porphyra umbilicalis*) and the Chlrophyta *Ulvaria obscura*. In this study the maximum growth rate was found in tests with solar radiation excluding UV radiation. *Ulvaria obscura* appeared to be the most sensitive to *in situ* levels of UV-B radiation, reducing its growth to 54%. The lower sensitivity was recorded in *Fucus vesiculosus.* Makarov (1999) also described May as a critical period for algae, which were highly affected by ultraviolet radiation during this month.

The apical segments of the intertidal macroalga *Hypnea musciformis* (Rhodophyta, Gigartinales) cultivated *in vitro* free of UV radiation showed growth rates of 9.7% day^{-1}, while algae exposed to UV-B grew only 3.2% day^{-1} (Schmidt et al., 2012).

Different growth rates were found for *Chlorella* sp cells when irradiated with 30 kJ m^{-2} UV-B as compared to unirradiated cultures: the specific growth rate immediately after the lag phase was 0.36±0.06 and 0.26±0.03 day^{-1} for unirradiated cultures and cultures irradiated with UV-B respectively (Estevez et al., 2001). Andreasson and Wängberg (2007) showed the effect of UV-B radiation on growth rate for two marine microalgae: *Dunaliella tertiolecta* (Chlorophyceae) and *Phaeodactylum tricornutum* (Bacillariophyceae). The growth rate of *D. tertiolecta* was slightly more inhibited by UV-B radiation than was the growth rate of *P. tricornutum*, with the same wavelength dependencies.

A growth-related temperature dependence of sensitivity to UV-B radiation was suggested by Altamirano et al. (2003) based on germling of three species of *Fucus* (Fucales, Phaeophyta): *F. spiralis* (eulittoral), *F. vesiculosus* (eulittoral-high sublittoral) and *F. serratus* (high sublittoral). Altamirano et al. (2003) determined the effects of different ultraviolet radiation conditions, UV radiation doses and temperatures on the relative growth rates of germlings of three species of intertidal brown macroalga. High ultraviolet-B radiation levels and low temperature, as independent factors, led to a species-specific reduction in RGR which appears to be related to the vertical distribution of the species in the intertidal zone. The inhibition of RGR ranged from 10% to even death of the germling. For the most sensitive species, high temperature in combination with a high dose of UV-B caused the death of the germlings, whereas at low temperatures germlings were able to survive.

In *Gracilaria lemaneiformis* UV radiation resulted in an insignificant impact on growth, because the presence of UV-A enhanced the relative growth rate, while UV-B inihibited it (Xu and Gao, 2010).

Sensitivity

The sensitivity to UV appears to be related with natural UV-irradiance of the environment for the same species (Marshall and Newmann, 2002). This work shows that isolates of the marine microalga *Chattonella marina* (Raphidophyte) from Australia exhibits higher tolerance to high intensities of visible light than *C. marina* collected from Japan waters. This microalga is known to cause wild and

farmed fish mortality in Japanese and South Australia waters (Marshall and Newmann, 2002).

The UV-B sensitivity is also related to life cycle stage. Cordi et al. (2001) observed that zoospores of the green intertidal macroalga *Enteromorpha intestinalis* were six fold more sensitive to UV-B exposure than mature talli. Cordi et al. (2001) also observed a greater sensitivity in the sexual reproductive phase of the life cycle of this macroalga species compared with the asexual phase. Inhibition of germination success and growth rates of settled gametes and zoospores after 1-h exposure to elevated levels of UV-B (equivalent to 27 and 31% ozone depletion) showed that damage to the reproductive cells was irreversible.

Most of the studies are concerned with high sensitivity of algae (micro and macro algae) species to UV radiation, showing the deleterious effects of these wavebands on cell integrity. Nevertheless Holzinger et al. (2009) reported that organelles like mitochondria, Golgi bodies and the nucleus of the vegetative freshwater green alga *Zygnema* remained unaffected by the radiation exposures, showing to be well adapted to ambient solar radiation and enabling the alga to cope with experimental UV exposure. According to the authors this effect is expected to persist in a scenario of enhanced UV radiation caused by stratospheric ozone depletion. *Nodularia spumigena*, a freshwater cyanobacterium, is a species that in general is not negatively affected by moderate levels of UV-B radiation (Wulff et al., 2007).

Algae from high mountains lakes, naturally exposed to high levels of UV radiation, show high UV resistance. Phytoplankton species with high resistance to increasing UV radiation have probably more adaptive capacity to survive in regions of increasing UV and tend to raise the number of individuals, reducing species biodiversity of phytoplankton communities.

So, some species are tolerant or even show stimulation when exposed to UV-B radiation, while some are highly susceptible.

Photosynthesis and photosynthetic pigments

Photosynthesis

Among various physiological processes, photosynthesis is potentially the main target of UV radiation due to a multiplicity of possible effects (Holzinger and Lütz, 2006). UVR inhibits photosynthesis, damages DNA and proteins and affect algae morphology. Jones and Kok (1966) study was the first to demonstrate the potential of UV to inhibit photosynthesis (references in Hanelt and Roleda, 2009). The UVB inhibition spectrum corresponds much more with the spectral absorption by DNA and proteins than photosynthetic pigments one (Hanelt and Roleda, 2009). Photosystem II (PSII) is a primary UV-B target (Aro et al., 1993 referred by Bouchard et al., 2008). Photosystem I (PSI) is relatively insensitive to UV-B damage (Strid et al., 1990 referred by Bouchard et al., 2008). In PSII, several possible sites of damage are associated with the D1 protein, one of the key proteins involved in a PSII repair cycle (Aro et al., 1993 referred by Bouchard et al., 2008). The primary enzyme involved in CO_2 fixation, ribulose-1,5-bisphosphatase carboxylase-oxygenase (RuBisCO), is also a suspected target of UV-B inhibition (Kumar et al., 2003; Bouchard et al., 2008). Both PSII and Rubisco have been shown to be affected by UV-B radiation (Bouchard et al., 2008). UV-B exposure may cause the loss of photosynthetic pigments (Bischof et al., 2000; Lütz et al., 2005, referred by Holzinger and Lütz, 2006), and reduce the expression of genes involved in photosynthesis (Mackerness et al., 1999 as referred by Holzinger and Lütz, 2006).

The harmful blooming raphidophyte *Chattonella subalsa* and dinoflagellate *Prorocentrum minimum*, showed a significant decline in the photochemical capacity of photosystem II (PSII), F_v/F_m (vitality indicator) in both algal species when shifted to high light, with a greater decline noted in *P. minimum*. This study also showed a rapid reduction in electron transport with an increment immediately after light exposure (Warner and Madden, 2007).

The biological weighting function (BWF) describes the effectiveness of the different wavelengths to produce biological responses, such as inhibition of photosynthesis (Andreasson and Wängberg, 2006). So, high light intensities may result in an inhibitory effect on metabolic processes. Photoinhibition will be defined as the generic outcome of the failure of photoprotection to mitigate photoinactivation, which occurs when damage of reaction centre proteins exceeds photorepair of photosystem II (Hanelt et al., 2006).

UV-B radiation may ameliorate photoinhibition in specific shallow water on tropical marine macrophytes (Hanelt and Roleda, 2009): brown algae (*Dictyota* sp., *Padina sanctae-crucis*, *Lobophora variegata*, *Sargassum polyceratium* and *Turbinaria turbinate*), the green algae (*Udotea flabellum* and *Halimeda discoidea*) and the seagrasses *Syringodium filiforme* and *Thalassia testudinum*.

Coccolitophores of *Emiliana huxleyi* species

exposed to solar UV radiation (UVR, 280-400 nm) showed a significant decrease in the rates of photosynthesis and calcification (Guan and Gao, 2010). Shorter wavelengths of UV-B led to more damages to photosynthetic apparatus than to calcifying machinery, while longer wavelengths of UV-A results more harmful to calcification. During long term exposures to solar radiation, the ratios of repair to UV—related damage increased indicating an acclimation to UV. UV—induced stress led to a protective strategy of *E. huxleyi*, sacrificing the growth by allocating energy for accumulation of UV-absorbing compounds and calcification (Guan and Gao, 2010).

Two frequently used techniques for measuring photosynthetic capacity in planktonic producers are: pulse-amplitude-modulation (PAM) fluorescence from Photo System II (PSII), and fixation of ^{14}C-labelled carbom dioxide. The first measures the function of the light-harvesting complexes, the reaction centres and the following electron transport. The second measures actual carbon fixation by Rubisco, which depends both on a functional photosynthetic electron transport and on the enzymatic reactions within the Calvin-Benson cycle. The PAM technique has considerable advantages being both cleaner and easier to perform and can be done unobtrusively (Andreasson and Wängberg, 2006). Measures indicatives of vitality are F_v/F_m and chlorophylls/phaeopigments ratio (Arróniz-Crespo et al., 2008). The rapid decreases in F_v (variable chlorophyll fluorescence) in response to increasing UV-B radiation, in addition to the fact that F_v decreased in a dose-dependent manner to UV-B, indicated that F_v may be a suitable, sensitive biomarker for UV-B exposure (Cordi et al., 2001).

Photosynthetic efficiency by the intertidal red alga *Porphyra umbilicalis* was related to immersion period and not to sun exposure (Sampath-Wiley et al., 2008). Immersion period was the greater facilitator of photoinhibitory damage and ROS generation at PSII. Authors conclude that protection via elevated antioxidant metabolism and increased PSII repair are involved in providing relief from the acute environmental stresses in the intertidal zone.

Antarctic waters indicate a reduction in photosynthesis of around 25% in the top 10-20 m due to increased UV-B radiation (reference in Malanga et al. 1999), which can compromise sustainability as a serious deregulations in trophic webs.

Photosynthetic pigments

There are basically three classes of photosynthetic pigments in algae: Chlorophylls, carotenoids and phycobilins. Chlorophylls are greenish pigments that contain a porphyrin ring. The most important is Chlorophyll *a* present in all plants, algae and cyanobacteria that photosynthesize. Chlorophyll *b* occurs only in green algae and in plants. Chlorophyll *c* is found only in the photosynthetic members of the Chromista as well as the dinoflagellates. Carotenoids are usually red, orange, or yellow pigments and include the familiar compound carotene. They are called accessory pigments because they cannot transfer energy directly to the photosynthetic pathway, but pass their absorbed energy to chlorophyll. One very visible accessory pigment is fucoxanthin, the brown pigment which colours kelps and other brown algae as well as the diatoms. Phycobilins are water-soluble pigments occurring only in cyanobacteria and Rhodophyta (red algae).

The damaging effects of UV radiation on the pigments are dependent on the UV wavebands and the exposure time (Döhler and Lohmann, 1995; Huovinen et al., 2006). UV-B induces the reduction of the number of phycobilisomes per cell in cyanobacteria (Araóz et al. 1998) and according to Häder et al. (2004) UV wavebands induce a bleaching of all pigments in rhodophyta. Contents of chlorophyll a and $c_1 + c_2$ were mainly reduced by UV-A of high intensity and by UV-B (Araóz et al. 1998). β-carotene seems to be the most sensitive pigment (Döhler and Buchmann, 1995) to UV radiation exposure. Exposing the marine haptophycean *Pavlova lutheri* and *Pavlova* spec., Döhler and Buchmann (1995) showed a reduction in fucoxanthin content and an increased in neofucoxanthin and chlorophyll c. According to these authors, the UV-induced increase in neofucoxanthin can probably be explained by a stimulation of the biosynthesis and degradation of fucoxanthin. No damaging effect on pigments was found after UV-A exposure of low intensity. Pools of glutamine, glycine, threonine, and phenylalanine were enhanced and that of glutamate reduced.

Following UV exposure, phycoerythrin (PE) fluorescence emission increases dramatically in *Nostoc* species, indicating accumulation of PE in the phycoblilisome rods (Wang et al., 2007, 2008). Nevertheless, phycoerythrin (PE) and phycocyanin (PC) in rhodophytes decrease with UV exposure (Schmidt et al., 2009) like is confirmed in *Porphyra umbilicalis* (Aguilera et al., 1999), *Gracilaria*

lemaneiformis (Xu and Gao, 2010) and *Hypnea musciformis* (Schmidt et al., 2012).

UVR did not affect the content of Chl *a* in *Gracilaria lemaneiformis* (Xu and Gao, 2010), but in the intertidal red macroalga *Porphyra umbilicalis* Chl *a* decreased by 65-67% and carotenoids showed a decrease by 75-82% (Aguilera et al., 1999).

Coralina elongata Ellis and Soland by Häder et al. (1997) study showed that Chl *a* and PE (phycoerythrin) were higher in the shade than in the sun type algae, but the two pigments did not show the same variation troughout the day. Both the depletion and recovery of this pigment were higher in the shade morphotype. The concentration of PC (phycocyanin) was very low compared with PE and only in the sun morphotype there was a significant depletion of this pigment. The concentration of SP (soluble protein) was similar in the sun and shade type algae, coinciding with the depletion of PE, PC and oxygen production. The ratio PE to SP was higher in the shade than in the sun type algae.

Studies of Huovinen et al. (2006) with the red alga *Grateloupia lanceolata* showed a decline on photosynthetic activity, phycobiliproteins and internal nitrogen content. Nevertheless these authors observed beneficial effect of UVR on recovery or photoprotective processes under enriched nitrogen conditions, but not on MAA pattern.

The brown alga *Chondrus crispus* (Phaeophyta) collected from the subtidal zone (6 m depth) increased the concentration of carotenoids with repeated exposures to UV-radiation (Yakovleva and Titlyanov, 2001). Prolonged exposures to high irradiance induced a substantial decline in the potential quantum yield of photosynthesis (F_v/F_m) and progressive pigment destruction responsible for stress damage (Yakovleva and Titlyanov, 2001). Photoinhibition of F_v/F_m exceeded 95% of control. Even after 20h under low radiance, F_v/F_m was similar to values measured immediately after stress, indicating severe photo damage (Yakovleva and Titlyanov, 2001).

Buoyancy

Buoyancy in aquatic photosynthetic organisms is essential in order to maintain them in water trophic layers for photosynthesis, reproduction and survival. In cyanobacteria, buoyancy is provided by gas vesicles that play an important role in regulating vertical distribution and nutrient acquisition (Ma and Gao, 2009). PAR (λ=400-700 nm) drives photosynthesis, but also results in photoinhibition at high levels. On the other hand, reduced levels of UVR might act as cues controlling vertical migration and enhance photosynthetic carbon fixation by phytoplankton (Ma and Gao, 2009). Ma and Gao (2009) studying *Arthrospira (=Spirulina) platensis* (important economic cyanobacterium) observed that floatation activity decreased with increased photosynthetic rates associated with increased photosynthetically active radiation (PAR), but it decreased less in the presence of UVR, which resulted in inhibitory effects (Ma and Gao, 2009). In this study, when the cells were grown under isoenergetic levels of solar PAR or UVR alone, they migrated downward under PAR but maintained buoyant under UVR. The buoyancy regulation of this photosynthetic cyanobacterium depended on the exposed levels of PAR as well as UVR, which affected photosynthesis and growth in an antagonistic way (Ma and Gao, 2009). The authors conclude that the buoyancy of *A. platensis* in water columns is likely to be dependent on diurnal photosynthetic performance regulated by solar radiation, and can hardly be considered as an active strategy to gain more energy during sunrise/sunset or to escape from harmful irradiation during the noon period.

Protein and DNA damage

Specificic studies related to DNA damage effects of UV-B exposure on cyanobacteria, micro and macroalgae were performed by Buma et al. (2001), Fabanđel et al. (2001), Sinha and Häder (2002), Kumar et al. (2004), Häder and Sinha (2005), Helbling et al. (2008), Rastogi et al. (2011) and Chen et al. (2012).

Nucleic acids absorb and are damaged by solar UV (Häder and Sinha, 2005), which attributes adverse effects on living systems (references in Rastogi et al., 2011). The two major UV-induced DNA lesions are directly by the formation of cyclobutane-pyrimidine dimers (CPDs) and pyrimidine (6-4) pyrimidose photoproducts (6-4PPs, pyrimidine adducts) and their Dewar valence isomers (references in Häder and Sinha, 2005) that can alter the molecular structure of genome leading to chronic mutagenesis and cell death (references in Rastogi et al., 2011). Indirectly effects occur via the production of ROS (references in Rastogi et al., 2011). Oxidative stress, acting synergistically with UVR (Dahms and Lee, 2010) usually results in single- as well as double-strand breaks (DSBs) in the native DNA molecule, causing extensive DNA damage. UV-A waveband, in comparison to UV-B, has poor efficiency in inducing DNA damage because native DNA does not absorb them (Häder and Sinha, 2005). However, UV-A or visible light

photon (up to 670-700 nm) is still able to induce DNA damage either by producing a secondary photoreaction of existing DNA photoproducts or via indirect photosensitization reactions (references in Rastogi et al., 2011).

Methods for detecting DNA damage in algae are briefly described by Häder and Sinha (2005) but new proposals were published after them. UV-induced DNA degradation may be analysed by using radioactive methods (O'Brien et al., 1982 referred by Häder and Sinha, 2005) to determine DNA degradation in terms of a decrease in radioactivity lost from DNA. Freeman et al. (1986) (referred by Häder and Sinha, 2005) proposed a non-radioactive alkaline agarose gel method to determine single-strand breaks in nanogram quantities of DNA. UV-induced cyclobutane dimers can also be identified and quantified by using specific antibodies (Roza et al., 1988, Mitchell et al., 1991, Mori et al., 1991 as referred by Häder and Sinha, 2005). Detection of CPD may also be performed following Li and Waters (1996) method by using oligonucleotides and magnetic beads which label DNA fragments, cut at the dimers and chemical sequencing reference ladders (Häder and Sinha, 2005). Another method employs an endonuclease to cleave the DNA at the CPDs; the resulting fragments are then subjected to gel electrophoresis with subsequent image analysis to determine the length of the fragments and the frequency of CPDs per megabase pairs can then be calculated by a method designed by Quaite et al. (1992) (Häder and Sinha, 2005); Douki et al. (2000) proposed an immune-dot-blot assay technique to detect CPDs, 6-4PPs and their Dewar valence isomers after UV radiation (Häder and Sinha, 2005); Sinha et al. (2001) (as referred by Häder and Sinha, 2005) used a simple and efficient quantitative method to determine the frequency of thymine dimers in a variety of organisms such as cyanobacteria, phytoplankton and macroalgae by using thymine dimer-specific antibodies followed by blotting and chemiluminescence methods. Electrospray-mass spectrometry (Douki et al., 2000a referred by Häder and Sinha, 2005) and high performance liquid chromatography-tandem mass spectrometry (HPLC-MS) was devised to quantify thymine dimers (Douki et al., 2000b, referred by Häder and Sinha, 2005). Fanfanđel et al. (2001) proposed a specific detection of cyclobutane pyrimidine dimers in phytoplankton by a non-radioactive assay based on T_4-endonuclease V digestion; the quantification of CPDs is estimated by alkaline agarose gel electrophoresis. Kumar et al. (2004) proposed a method for detection of DNA damage in cyanobacteria by PCR assay. According to Häder and Sinha (2005) this method may not be sufficient to detect the formation of CPDs, 6-4PPs and their Dewar valence isomers in an organism after UV radiation. Chen et al. (2012) used a fluorometric analysis of DNA unwinding (FADU) as described by He and Häder (2002) and modified by Chen et al. (2009).

Phototoxicity

Direct effect of UVR exposure on biological macromolecules including DNA is called photosensitization, and generally leads to the production of singlet oxygen or other ROS that are highly damaging to biomolecules (Chen et al., 2006 referred by Dahms and Lee, 2010).

Photomodification results in the formation of new compounds that exhibits greater toxicity than the parent phototoxicant (Brack et al., 2003), being an indirect effect of UVR on biomolecules. Photomodification results in photoenhanced toxicity. Polycyclic aromatic hydrocarbons (PAHs), pesticides, herbicides or antifoulings are examples of phototoxic compounds. The toxicity of oil products, weathered oil and specific polycyclic aromatic compounds increases 2 to greater than 1000 times in the presence of UV (references in Barron and Ka'Aihue, 2001). Pesticides (Bhattacharyya, et al., 2011) and herbicides (Chen et al., 2012) are carried out to water bodies (to freshwaters and then to marine system) through run-off, drift and leaching increasing the risk of exposure in non-target organisms in which, under UV exposure, another photoenhanced toxicity may occur, disrupting the dynamics of the ecosystems. The combination of Tributil-tin (TBT) and UV-B radiation stresses also have synergistic effects affecting the first trophic level of the marine food web (Sargian et al., 2005).

Nutrients uptake

The cycling of key elements like carbon (C), nitrogen (N) and phosphorous (P) in aquatic systems depends to a large extent on productivity and fate of autotrophs. Several works demonstrated an inverse effect of UV radiation and PAR with regard to elemental ratios, notably C:P. Uptake rates of ^{15}N-ammonium of algae is affected by UV-A of high intensity and UV-B radiation. The results also show a significant reduction in total nitrate by 95.5% in the high UV-B treatment (Döhler and Buchmann, 1995; Braune and Döhler, 1996; Anusha and Asaeda, 2008). The recovery of photosynthetic activity and phycobiliproteins, was

enhanced in the algae previously incubated under PAR + UVR as compared to exposure to only PAR, suggesting a beneficial effect of UVR on recovery or photoprotective processes under enriched nitrogen conditions (Huovinen et al., 2006).

Significant increase in dissolved ammonia in water under UV-B exposure, due to photoxidation and bacterial decomposition of organic nitrogen in the system, alter the natural balance of nitrogen, oxygen and dissolved carbon in aquatic systems.

Nutritional quality

Polyunsaturated fatty acids (PUFAs) play a key role in aquatic food webs because only photosynthetic organisms synthesize them and they are essential macromolecules for heterotrophs. PUFAs are also of major importance in regulating membrane fluidity under low temperatures. Several studies have documented a negative impact of UV radiation (280-320 nm) on PUFAs (polyunsaturated fatty acids) in marine phytoplankton species: this impact has been attributed either to oxidation of previously synthesized fatty acids or to disruption of their synthesis (references in Leu et al., 2006).

Temperature is a crucial parameter, since it may have a substantial impact on fatty acid composition itself as well as on the dynamics of repair mechanisms. An initial increase in PAR intensities profoundly affected the fatty acid composition and substantially inhibited the synthesis of PUFAs, but the relative amounts of PUFAs were not reduced by UV radiation in the diatom *Thalassiossira antarctica* var. *borealis* (Leu et al., 2006). Enhanced UV radiation did cause a significant reduction in optimum quantum yield of PSII and affected some fatty acids, mainly 18:0 and 16:1 n-7. Both ambient and enhanced UV radiation caused significantly lower C:P and N:P ratios. A higher relative content of the photoprotective pigments diadinoxanthin and diatoxanthin was observed. The diatom *T. antarctica* var. *borealis* showed that brief periods with high light exposure may cause significant changes in photosynthetic activity and food quality, but the capacity for photo-acclimation seems high. The impact of UV radiation seems to be less important for food quality than that of PAR during a sudden rise in total light intensity.

Indirect UV-radiation harmful effects

Few studies are deal with indirect harmful effects of UVB. The first experimental evidence of indirect UVB effects on reproductive output through trophic response in marine plankton conducted by Kouwenberg and Lantoine (2007). In this experiment both control and UVB-stressed of a common marine diatom *Skeletonema costatum* cultures were used as food for wild pelagic copepod *Calanus helgolandicus* females collected in the NW Mediterranean. This study showed that female copepods fed on control diatoms produced three times more eggs and healthier offspring with fewer lethal naupliar deformities than those fed on UVB-exposed diatoms.

Conclusions

Photosynthetic organisms support life on Earth, and aquatic biophotosystems contribute with 50% of the global oxygen supply of all life.

A study of the effects of UV radiation is complex because the organisms face different stressors, making it difficult to identify the real magnitude of the harmful effects of ultraviolet radiation in wild communities and ecosystems.

Species with low capacity of living under UV irradiation due to their repair unability tend to disappear, unbalancing the ecosystem and reducing biodiversity.

Numerous information is available about UVR photobiology, particularly since the awareness of ozone depletion. Long term consequences of UVR exposure on organisms and its consequences in the ecosystems balance are still uncertain. High ROS formation rates are particularly important especially for organisms with early life stages in the plankton from surface waters dwelling at certain environmental conditions (cloudless sky, thin ozone layer, lack of wind, calm seas, low nutrient loading).

Ecological significance of elevated UV-B exposure in the aquatic environment may be seriously underestimated if effects on the early lifestages of algae are not considered.

Synergisms among stressors are shown to be increasingly important in the face of global environmental change and must consider both, the effects of UV-B on a sinlge species and its effects on entire communities and systems (Dahms et al., 2011).

Increasing growth rates in species resistant to UV exposure, like the forementioned raphidophyte microalga (*Cattonella* sp), which is known to cause fish mortality in Japanese waters and was also implicated in mortality of farmed finfish in South Australia, may also have important economic negative impacts on aquaculture industry

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