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**REVIEW ARTICLE**

# Algae and aquatic macrophytes responses to cope to ultraviolet radiation – a Review

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**Abstract**

UV radiation became an important issue since the awareness of the ozone hole in Antarctida and its relationship between the human activity, the depletion of the protecting layer, and the effects of ultraviolet radiation in the biological relevant wavebands on algae and on organisms in general. All aquatic organisms are depended on algae and aquatic plants (submerged or near shallow line) for food, shelter, also as oxygen supplement and CO2 sequestration by photosynthetic procedure. So, a disturbance in this trophic layer creates a global unbalancing. Harmful effects of UV, especially UV-B were intensibly studied under laboratory and field studies, and reported in scientific reports from a large team of scientists. UV- induced repair mechanisms allowing the survival of certain species under UV irradiation is also largely documented in algae species, and in phytoplankton of the entire aquatic systems (freshwater, marine and brackiswater). 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) concerning the strategies of protection developed by aquatic photoauthotrophs (micro and macroalgae, and aquatic macrophytes, like seagrasses and liverworts) to fit under these wavebands of radiation. 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 marine and freshwater plants exposed to UV irradiation.

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

*Abbreviations:* APX - ascorbate-peroxidase; CAT – catalase; CCs – chlorocarbons; CFCs- chlorofluorocarbons; CPDs - cyclobutane pyrimidine dimers; DAD – diode array detection; DHAR - dehydroascorbate reductase; GR - glutathione reductase; HPLC/MS - high-resolution reverse-phase liquid chromatography and mass spectrometry; hsp70 - Heat shock protein; HSPs - Heat shock proteins; Huv - high dosage of UV-B irradiation; Luv - low dosage of UV-B irradiation; M-xxx – chemical structure not identified of mycosporine-like amino acids detected at xxx nm; MAAs - mycosporine-like amino acids; MCF - methyl chloroform; MD-HAR - monodehydroascorbate reductase; MDHA – monodehydroascorbate; Muv - medium dosage of UV-B irradiation; NAC - N-acetylcysteine; NER - nucleotid excision repair; NOx – dioxins; OBS – organobromides; P334 - Porphyra-334; PER - photoenzymatic repair; PFD - photon flux densities; POX – peroxidase; PUFAs - polyunsaturated fatty acids; ROS - reactive oxygene species; SH – shinorine; SOD - superoxide dismutase; TBARS - thiobarbituric acid reacting substance; UV-A - ultraviolet-A; UV-B - ultraviolet-B; UV-C - ultraviolet-C; UVR – ultraviolet radiation.

## Introduction

High increase industrialization in the past few decades resulted to an increase in anthropogenically atmospheric pollutants such as chlorofluorocarbons (CFCs), halocarbons, chlorocarbons (CCs), organobromides (OBS), carbon dioxide ($CO_2$), methyl chloroform (MCF) and dioxins ($NO_x$) is being related to the depletion of the UV-screening ozone layer in the stratosphere (references in Singh et al., 2010b).

With the shallowing ozone layer, UV radiation is increasing not only in Antarctida zone but also all over the Earth' surface, penetrating into water in depht according to multiple factors.

Algae and photosynthetic macrophytes are the support of entire life because all aquatic organisms are dependentd on their production for food, shelter, also as oxygen supplement and $CO_2$

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sequestration by photosynthetic procedure and as regulators of pH.

Sun radiation is crucial for photoautotrophs and is composed by UV radiation ($\lambda_{max}$ = 200 to 400 nm), visible radiation ($\lambda_{max}$ = 400 to 750 nm) and infrared radiation ($\lambda_{max}$ >750 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 allows photosynthesis process by photosynthetical organisms.

The harmful effects of UV radiation on biota from marine, freshwater and terrestrial habitats are extensibly documented. Reducing primary productivity, plankton composition (Davidson et al., 1996) and denitrification inhibition (Mancinelli and White, 2000) are among deleterious effects of UV in aquatic communities. UV radiation in algae (including cyanobacteria) inhibits growth and development (Gao and Ma, 2008), biomass, productivity, photosynthesis, buoyancy (Gao and Ma, 2008; Helbling et al., 2008; Sampath-Wiley et al., 2008; Zeeshan and Prasad, 2009; Dahms and Lee, 2010; Dahms et al., 2011). As it is a stress mechanism, usually a series of reactive oxygene species (ROS) is formed that in part mediate DNA damage, mutagenesis, cellular aging, carcinogenesis and apoptosis (Downs et al., 2002; He and Häder, 2002; Häder and Sinha, 2005; Dahms and Lee, 2010; Rastogi et al., 2011).

Effects of short-wavelength solar radiation in the UVrange (λmax = 280 to 400 nm) include DNA by-products, being the most significant cyclobutane pyrimidine dimers (CPDs), which comprise 70-90% of all aberrant DNA photo-products. CPDs increase linearly with UV-B exposure, however the dose-relationship varies significantly between taxa (references in Dahms and Lee, 2010).

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).

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 may reach to depths to 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 Dahms 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 (UVR) 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).

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, all of which promote apoptosis, than exposure to UV-A (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). Moderate levels of UV-A may stimulate photosynthesis and growth in both micro and macroalgae (references in Xu and Gao,

2010). UV-C is the most damaging portion 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).

There are several important reviews on various aspects of UV radiation effects on aquatic ecosystems: aquatic ecosystems in general (Häder et al., 1998; Häder, 2000; Sinha and Häder, 2002a; 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., 2010a,b); 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 and responses (Jenkins et al., 1995; Glatz et al., 1999; Dahms and Lee, 2010; Dahms et al., 2011); ultraviolet sunscreens in dinoflagellates (Banaszak and Trench, 2001); the role of mycosporine-like amino acids in marine biota (Klisch and Häder, 2008; Pallela et al., 2010; Carreto and Carignan, 2011); methods for DNA damage detection (Sinha and Häder, 2002b); 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 (Williamson, 1995, 1996 as referred by 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 on the main mechanisms of protection to survive under UV irradiation, updating previous reviews.

## Mechanisms of protection against UV radiation

The young Earth, about $3.8x10^9$ years ago, received very high doses of UV-radiation. It is estimated that, at the time, the sun, like young T-Tauristars, emitted about 10 000 times more UV than at present (Canuto et al., 1982) referred by Rozema et al. (1997). The luminosity of the sun then was much lower than at present, resulting in temperatures below freezing (Rozema et al., 1997). Nevertheless, liquid water did occur, caused by atmospheric carbon dioxide ($CO_2$) levels 100 -1000 times higher than present values, which absorbed infrared radiation and created a pronounced greenhouse effect (Canuto et al., 1982, referred by Rozema et al., 1997). Release of $O_2$ by photosynthetic bacteria, cyanobacteria and eukaryotic algae led to a gradual increase of atmospheric $O_2$ and a concomitant decrease of atmospheric $CO_2$ (Rozema et al., 1997).

Cyanobacteria are primitive photosynthetic oxygen-evolving prokaryotes that appeared on the Earth when there was no ozone layer to protect them from damaging ultraviolet radiation (UVR). Cyanobacteria are the only known oxygenic phototrophs capable of fixing atmospheric nitrogen (reference in Giordanino et al., 2011) and probably those who have developed the more suitable mechanisms to avoid or minimize UVR stress.

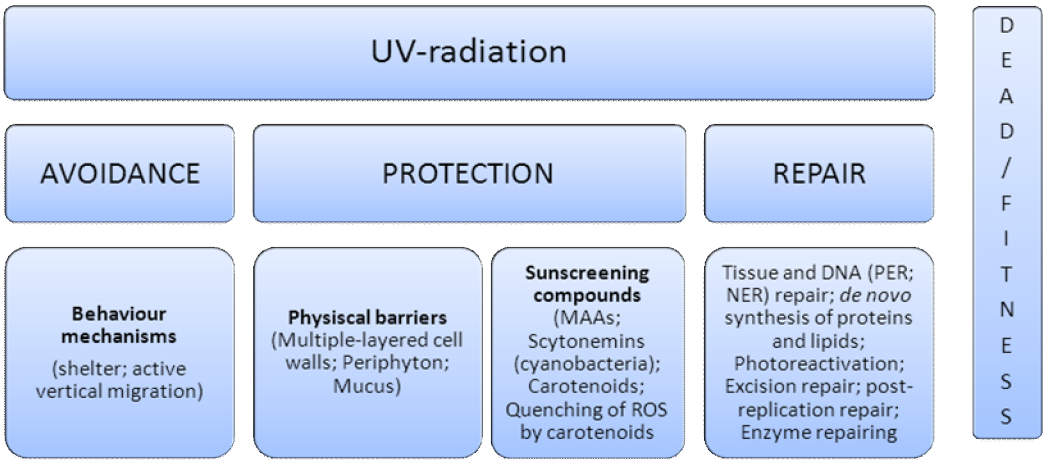


Figure 1. Mechanisms evolved by algae to cope with UV-radiation.
(based on Dahms and Lee, 2010; Dahms et al., 2011).

There are basically three different ways through which organisms have evolved to cope with UVR (Figure 1): avoiding it, protecting themselves, and repairing potential damage (reference in Dahms et al., 2011). Invertebrates avoid UVR by using sheltered and/ or deeper habitats (Dahms et al., 2011) and microalgae use self-mobility. Some develop protective coatings or make use of sunscreens while others repair damage occurred by UVR (Dahms et al., 2011). Often, these natural mechanisms are triggered by visible light intensities where they might not protect against an increase in the ratio of UVR to visible light.

Living organisms exposed to high natural UV radiation have developed a suite of mechanisms to avoid or minimize UVR stress which include vertical migration, multiple-layered cell walls, or synthesis of protecting compounds such as carotenoids, mycosporine-like amino acids (MAAs), scytonemines (only cyanobacteria), proteins and some repairing enzymes.

**Behaviour mechanisms**

Free living microalgae such as dinoflagellates (Banaszak and Trench, 2001) and *Euglena gracilis* (Bolige and Goto, 2007) employ positive phototaxis at low radiances and a very accurate negative gravitaxis to swim towards the surface in order to receive a sufficient amount of solar radiation for photosynthesis procedure. However, during times of excessive radiation in order to reduce damage by surface UVR and PAR, light-mediated behaviour may influence the distribution of some cellular organisms to greater depths within the water column (Banaszak and Trench, 2001), by moving down into the water column guided by negative phototaxis.

Studies of Marshall and Newman (2002) with *Chattonella marina* (a marine fitoplankton – Radiophyceae – suggests that Japanese strain (not suitable for high UV exposure) may need to vertically migrate in the turbid waters to avoid UV exposure. *C. marina* is a subsurface bloom forming, highly motile flagellate, capable of active vertical migration. The cyanobacteria *Phormidium uncinatum*, *Anabaena variabilis* and *Oscillatoria tenuis* also migrate from the water surface to lower levels in order to avoid high solar irradiance (Donkor and Häder, 1995).

Vertical mixing may aid in recovery from photo damage by transporting phytoplankton away from high UVR toward low PFD (photon flux densities) where repair processes can proceed without incurring further damage. This movement down reduces productivity as a result of being deeper in water column versus repairing damage to the photosynthetic apparatus caused by UVR or high PFD (Banaszak and Trench, 2001). However, Hernando and Ferreyra (2005), exposing cells of a bloom forming diatom *Thalassiossira* sp., to variable light conditions, during one of the field experiments when ozone was low, observed a significant reduction in photosynthesis, suggesting that vertical mixing may not be efficient enough to prevent harmful UV-B radiation effects.

**Physical mechanisms (barriers)**

**Multiple-layered cell walls and mucilaginous sheath layer**

When exposed to artificial UVR some dinoflagellates (Banaszak and Trench, 2001) may produce a physical or chemical barrier to offset the deleterious effects of this radiation. The symbiotic dinoflagellate *Symbiodinium californium* (Banaszak and Trench, 2001) develops a multiple-layered cell walls and this phenomenon disappears after the cells were returned to culture conditions in the absence of UVR (Banaszak and Trench, 1995).

Mandal et al. (2011) showed that the presence of thick mucilaginous sheath layer was among the adaptation mechanisms that allowed the intertidal cyanobacteria *Lyngbya majuscula* to withstand prolonged UV-B radiation.

**Periphyton**

Periphyton (algae, bacteria, mucus, sediment particles, etc) is considered detrimental to inshore seagrasses (e.g. *Zostera marina, Ruppia marina*) as it reduces the amount of light, i.e. photosynthetically available radiation (PAR), that reaches the plant surface (Brandt and Koch, 2003).

Seagrasses, such as *Zostera* and *Ruppia* spp. are a functional group of approximately 60 species of underwater marine vascular plants (Lee, 2007). They constitute habitat for a great number of animal species like fish and shellfish and they are also important nursery areas. Filtering coastal waters, dissipating wave energy and anchorage of sediments are among the important physical functions of seagrasses.

The ecological importance of periphyton on seagrass leaves has been listed as: primary producer in seagrass systems; source of food and sediment particles (calcareous algae); environmental indicator of water quality (Borowitzka and Lethbridge, 1989 referred by Brandt and Koch, 2003); UV-B filter (Brandt and Koch, 2003).

Algae as well as detritus are contributing to the reduction of light transmittance through the periphyton layer (Brandt and Koch, 2003). The strong absorption (reduced transmittance) in

wavelengths characteristic of chlorophyll *a* (430 and 663 nm) and carotenoids (401-518 nm) suggest that photosynthetic organisms are contributing to light attenuation.

Periphyton accumulation on seagrasses leaves may provide an effective UV-B filter, a factor that may be especially important in tropical marine oligotrophic waters in which UV penetrates relatively deep into the water column (Brandt and Koch, 2003). The higher transmission in the PAR than in the UV-B range allows the seagrasses to receive a higher proportion of beneficial light while reducing the detrimental radiation (Brandt and Koch, 2003). According to authors, this beneficial effect of periphyton as a UV-B filter is lost when PAR transmission reaches levels that strongly limit photosynthesis.

**Production of photoprotective compounds**

Sunscreening compounds protect the organism against UVR damage. Such compounds are mycosporine-like amino acids (MAAs), carotenoids, and antioxidants.

Usually UV-absorbing compounds and carotenoids increase in response to exposures with UVR, as it happens to the diatom *Skeletonema costatum* (Wu et al., 2009).

**Mycosporine-like amino acids (MAAs)**

MAAs are ultraviolet-absorbing molecules having absorption maxima between 320-360 nm (reference in Carreto and Carignan, 2011). They are small (<400 DA), colorless, water-soluble compounds (Sinha et al., 2007), being imine derivatives of mycosporines, which contain an amino-cyclohexenimine ring linked to an amino acid, amino alcohol or amino group (reference in Carreto and Carignan, 2011). Mycosporine-glycine and mycosporine-taurine are the only known aminocyclohexenones from marine sources (Carreto and Carignan, 2011).

Recent reports indicate that MAAs are widely distributed in marine, freshwater and terrestrial organisms taxonomically diverse (Bandaranayake, 1998), including sea anemones (Banaszak and Trench, 1995; Shick and Dunlap, 2002; Arbeloa et al., 2010), and, as referred by Carreto and Carignan (2011) they have been reported in gorgonians, corals, sponges, brine shrimp, sea urchins, starfish, holothurids, clams, ascidians and fish. MAAs may be transmitted to grazing organisms (e.g. Carefoot et al., 2000) by predatory habits from algae, or by symbiotic (corals, gelyfish) or bacterial association. The organisms have evolved the capacity to synthesize, accumulate and metabolize a variety of mycosporine-like amino acids.

Table 1 summarizes MAAs isolated by several scientific works from algae with maximum absorption ranging from 265 to 362 nm, some of them detected or partially characterized or are unknown MAAs, since no molecular formula was able to be identified. Its detection is a consequence of the development of more efficient high-resolution reverse-phase liquid chromatography and mass spectrometry (HPLC-MS) techniques. Pallela et al. (2010) and Carreto and Carignan (2011) are two examples of recent reviews concerning photoprotecting compounds in marine organisms. Pallela et al. (2010) review photoprotective compounds from algae and other marine sources for further elaborative research and their probable use in cosmeceutical and pharmaceutical industries. Carreto and Carignan (2011) is also a very usefull review since the authors describe the structure and physicochemical properties of MAAs and the modern methods used for their isolation and identification in marine biota.

A database on UV-absorbing mycosporines and mycosporine-like amino acids (MAAs) has been constructed and described by Sinha et al. (2007) providing information on various mycosporines and MAAs reported in fungi, cyanobacteria, macroalgae, phytoplankton and animals from aquatic and terrestrial habitats. It also contains information on biosynthetic routes of MAAs as well as on the absorption maxima and molecular structures of different mycosporines and MAAs, and according to authors can be found on http://www.biologie.uni-erlangen.de/botanik1/html/eng/ maa_database.htm.

MAAs have been implicated in many biochemical processes (Shick and Dunlap, 2002). Experimental evidence indicates that the major role of MAAs is to act as photo-protective UV filters and/or to act as antioxidants (Dunlap et al., 1986; Carreto et al., 1990; Dunlap and Shick, 1998; Shick and Dunlap, 2002; Carreto and Carignan, 2011). In addition, oxocarbonil-MAAs such as mycosporine-glycine (Dunlap and Yamamoto, 1995; Yakovleva and Hidaka, 2004) and mycosporine-taurine (Zhang et al., 2007) have antioxidant properties, capable of protecting against the cellular damage that high levels of reactive oxygen species (ROS) induced in organisms under different stresses (Carreto and Carignan, 2011). High concentrations of MAAs have been found in selected dinoflagellates, prymnesiophytes, cryptomonads, antarctic and artic diatoms, raphidophytes and macroalgae, especially among surface bloom forming species or bentic

macroalga exposed in intertidal shores and in dinoflagellates in symbiosis with coral communities. *In vitro* studies of various MAAs have also given support to this function by confirming the high photostability and also the release of heat to the medium as the main relaxation pathway of the photoexcited molecules (Conde et al., 2004, 2007; Carreto and Carignan, 2011).

Beyond their UV-screening properties, MAAs are described to have more characteristics, as described by Carreto and Carignan (2011), even though some of them are controversial or unsupported: they may contribute to osmotic regulation; they may act as regulatory metabolites of sporulation and germination; they may act as transducers of UV wavelengths to wavelengths utilizable for photosynthesis; they may act as "host factors", that induce release of photosynthate from endosymbiotic algae; they may play a role under desiccation or thermal stress in certain organisms; they can also act as an intracellular nitrogen reservoir; MAAs and pyrimidines may function as alarm cues in the defence secretions of the sea hare *Aplysia californica*. The discovery that MAAs can be chemical signals raises an entirely new direction for exploring their potential functions and evolution (reference in Carreto and Carignan, 2011).

MAAs production, as suggested by Marshal and Newman (2002), seems to be related to an ecophenotypic adaptation due to differing environmental conditions. The marine phytoplankton *Chattonella marina* collected from Australian and Japan exhibit differences in tolerance to high intensities of visible light: Australian strain (with high natural UV exposure) of *C. marina* produced around five times more UV-absorbing MAAs than the Japanese strain. Japanese strain was more vulnerable to UV-induced cell damage, inhibition of photosynthesis and growth, which may lead to higher cell death than in Australian strain.

Table 1. MAAs isolated from algae (macro and microalgae), including cyanobacteria, and each absorption maximum waveband.

| MAA | Waveband ($\lambda_{max}$) (nm) | Reference |
|---|---|---|
| Unknown UV-absorbing compound | 265 | Xu and Gao (2010) |
| Unknown UV-absorbing compound | 280 | Guan and Gao (2010) |
| Mycosporine-glycine | 308 | Carignan et al. (2009) |
| Unkown MAA | 310 | Klisch et al. (2001) |
| Palytine | 319 | Carignan et al. (2009) |
| Palythine | 320 | Klisch et al. (2001); Carreto and Carignan (2011) |
| Palythine-serine | 320 | Carignan et al. (2009); Carreto and Carignan (2011) |
| Palythine-threonine | 320 | Carignan et al. (2009); Carreto and Carignan (2011) |
| Palythinol | 320 | Carreto and Carignan (2011) |
| Palythine-threonine sulphate | 321 | Carreto and Carignan (2011) |
| Palythine-serine sulphate | 321 | Carreto and Carignan (2011) |
| Unknown MAA | 324 | Gröniger and Häder (2002) |
| Mycosporine-methylamine-serine | 325 | Carreto and Carignan (2011) |
| Mycosporine-methylamine-threonie | 330 | Carreto and Carignan (2011) |
| Mycosporine-glutamic acid-glycine | 330 | Carreto and Carignan (2011) |
| Asterina-330 | 330 | Kräbs et al. (2002); Carreto and Carignan (2011) |
| Unknown MAA | 331 | Klisch et al. (2001) |
| Unkown MAA | 332 | Gómez et al. (1998) |
| Palythinol | 332 | Kräbs et al. (2002) |
| Mycosporine-2-Glycine | 332 | Carreto and Carignan (2011) |
| Shinorine | 333 | Carignan et al. (2009); Carreto and Carignan (2011) |
| Shinorine | 334 | Klisch et al. (2001) |
| Porphyra-334 | 334 | Klisch et al. (2001); Carreto and Carignan (2011) |
| (*E*)-palythenic acid | 335 | Carreto and Carignan (2011) |
| Mycosporine-glycine-valine | 335 | Carreto and Carignan (2011) |
| (*Z*)-palythenic acid | 337 | Carreto and Carignan (2011) |
| Unknown MAA | 348 | Gómez et al. (1998) |
| Usujirene | 357 | Carreto and Carignan (2011) |
| Palythene | 360 | Kräbs et al. (2002); Carreto and Carignan (2011) |
| Euhalothece | 362 | Carreto and Carignan (2011) |

Recent studies reported by Coba et al. (2009) using Porphyra-334 + shinorine (P334+SH) isolated from the red alga *P. rosengurttii* showed that the topical application of P-334 + SH on the skin of the female albino hairless mice had a protective effect against UV-induced skin damage in mice and contributed to maintain the antioxidant defence system of the skin as well as expression of heat shock proteins *hsp70*, being a potential candidate for new natural sunscreens commercialization.

**MAAs detection and quantification techniques:**

HPLC followed by DAD identification and quantification is the commonly method used for MAA detection and quantification. A series of known masses of pure MAA standards are injected, and the resultant chromatographic peak areas are related to injected masses to yield a response factor for each MAA. The masses injected of each compound could be quantified using their specific extinction coeficients and the dilution factor but the extinction coefficient of some MAAs are not known yet (reference in Carreto and Carignan, 2011). In this case, the use of the extinction coefficient for the MAA that has the closest match in wavelength maxima, may aid in yielding a useful concentration estimate (reference in Carreto and Carignan, 2011).

**Distribution of MAAs in cyanobacteria, algae and seagrasses**

In most cyanobacteria able to synthesize MAAs these compounds consist of shinorine, porphyra-334 (Sinha et al., 1999, 2001, 2002, 2003; Wulff et al., 2007) and in some cases mycosporine-glycine (references in Carreto and Carignan, 2011). Sinha et al. (1999, 2001, 2002) reported that the cyanobacteria *Anabaena* sp. and *Nostoc comune* only synthesize the MAA shinorine. Unidentified MAAs were also detected in other cyanobacteria: M-315 in *Scytonema* sp (Sinha et al., 2001) and M-333 in *Nodularia spumigena* (Wulff et al., 2007). Details of the pathway and the enzymes involved in the biotransformation of primary MAAs in cyanobacteria remain to be elucidated (Carreto and Carignan, 2011).

Dinoflagellates were the earliest group in marine phytoplankton noting UV absorbance (Carreto and Carignan, 2011). *Amphidinium carterae* and *Heterocapsa triquetra* are two dinoflagellates producing only one MAA: mycosporine-glycine (Hannach and Sigleo (1998) for the first and M-335 (Wängberg et al., 1997) for the second. In *Alexandrium tamarense* Callone et al. (2006) identified eleven MAAs, being porphyra-334 and palythene the major compounds and in lower concentrations shinorine, mycosporine-glycine, palythenic acid, usujirene, palythine, palythinol, shinorine-methyl ester (M-333) and two unknown MAAs, M-320 and M335/360. MAAs in *Alexandrium escavatum* were porphyra-334, palythene, shinorine and usujirene, the last one characterisitic of surface waters phytoplankton species. *Gloeodinium viscum* contained porphyra-334, palythene and mycosporine-glycine (Banaszak et al., 2000). In *Gymnodinium linucheae* was identified mycosporine-glycine, shinorine and porphyra-334. *Gyrodinium dorsum* contained shinorine, porphyra-334, palythine, and also two more unidentified-MAAs (M-310 and M-331) (Klisch et al., 2001). In the dinoflagellate *Lingulodinium polyedra* porphyra-334, mycosporine-glycine-valine, palythine, palythinol and palythene were found (reference in Sinha et al., 1998). *Prorocentrum minimum* – a red tide dinoflagellate – synthesized shinorine and palythene (Sinha et al., 1998). *Prorocentrum micans* contained mycosporine-glycine, shinorine, porphyra-334 and asterina-330 (reference in Sinha et al., 1998). *Simbiodinium* MAA producing species contained the following MAAs, differing according species: *Simbiodinium* sp, mycosporine-glycine, shinorine, porphyra-334 and palythine (Banaszak et al., 2006); *Simbiodinium corculorum* contained shinorine, porphyra-334 and mycosporine-glycine (Banaszak et al., 2000); in *Simbiodinium microadriaticum* shinorine and porphyra-334 were detected (Banaszak and Trench, 1995), *Simbiodinium meandrinae* produced mycosporine-glycine and shinorine (Banaszak et al., 2000); in *Simbiodinium pilosum* Banaszak et al. (2000) mycosporine-glycine, shinorine and porphyra-334 were identified.

In Haptophyta (Primnesiophyceae) microalgae, Sinha et al. (1998) detected unidentified MAAs in *Phaeocystis pouchetti*. In the coccolithophor *Emiliania huxleyi* a new MAA was detected at 280 nm, but its chemical structure was not identified (Guan and Gao, 2010). The Raphydophyceae *Chattonella marina* was able to produce mycosporine-glycine, mycosporine-glycine-valine and shinorine (Marshall and Newman, 2002) after UV exposure.

The synthesis of MAAs was not part of the UVB response in several studied diatoms (references in Carreto and Carignan, 2011). In *Thalassiosira* sp. shinorine and porphyra-334 were found (Sinha et al., 1998) and other studies report

the absence of MAAs (Carreto and Carignan, 2011). Zudaire and Roy (2001) reported the synthesis of MAAs in *Thalassiosira weissflogii*. MAA signature for most diatoms consists on primary MAAs (porphyra-334, shinorine and mycosporine-2 glycine) (Carreto and Carignan, 2011). Nevertheless in *Corethron criophilum* the presence of the secondary MAAs palythine and palythene was reported (reference in Carreto and Carignan, 2011). *Pseudo-nitzschia multiseries* showed the presence of the unusual mycosporine-taurine, reported only in sea anemones (Carreto and Carignan, 2011).

In Ochrophyta microalgae, *Acetabularia mediterranea* synthesize shinorine, porphyra-334 and palythine (Sinha et al., 1998), and a reference from Sinha et al. (1998) considered asterina-330 and palythine as the only MAA produced by *Heterococcus brevicelullaris* and *Pseudococcomyxa* sp., respectively.

In microalgae chlorophyta, Xiong et al. (1999) registered *Coelastrum microsporum* as no MAA synthesizer and identified mycosporine-glycine, palythine, asterina-330, shinorine and porphyra-334 in *Ankistrodesmus spir, Chlorella minutissima, Enallax coelastroides, Pseudococcomyxa sp*. and in *Scotiella chlorelloidea. Chlorella sorokiniana* and *Scenedesmus* sp. showed M-302, M-292 as addicional MAAs (Xiong et al., 1999). Sinha et al (1998) detected shinorine only in *Enallax coelastroides, Scenedesmus* sp. and *Scotiella chlorelloidea.*

**Macroalgae**

Marine macroalgae are divided into three groups: green seaweeeds (Chlorophyta), red seaweeds (Rhodophyta) and brown seaweeds (Phaeophyta).

Most of the MAA-producing macroalgae belong to Rhodophyta, followed by Phaeophyta and only a few macroscopic green algae produce MAAs (Carreto and Carignan, 2011).

According to Hoyer et al. (2002), rhodophytes can be divided into three different physiological groups related to MAAs synthesis: a) species withough any traces of MAAs; b) species that contain MAAs in variable concentration dependent of environmental conditions; c) species always containing a stable and high concentration of MAAs.

Shinorine and porphyra-334 are the most common MAAs reported in macroalgae in species (tables 2, 3 and 4) collected from tropical to polar regions (references in Carreto and Carignan, 2011), but the MAA compositions of some intertidal red macroalgae may be more complex. Total MAA levels in *Palmaria palmata* (Rhodophyta) samples from shallow waters (1.5 m depths) were greater than those from deeper waters (3 m depths) (reference in Yuan et al., 2009). The same species, *Palmaria decipiens*, from references in Carreto and Carignan (2011) have more MAA compounds than *P. decipiens* analysed by a reference in Sinha et al. (1998), showing the previous more asterina-330, usujirene and the unusual M335/360. M335/360 was also identified by Callone et al. (2006) in the dinoflagellate *Alexandrium tamarense* as already forementioned.

Schmith et al. (2012) found in the intertidal rhodophyta *Hypnea musciformis* a production of MAAs and carotenoids when this alga was exposed to high levels of UVR. The phenolic compounds are also involved in protecting talus of this alga species against direct exposure to solar light radiation, especially UVR (Schmith et al., 2012). Pavia et al. (1997) had reported the same in the brown alga *Ascophyllum nodosum.*

Phaeophyta (Table 3) show shinorine and porphyra-334 as only MAA produced, and in *Fucus spiralis* only shinorine was present (Sinha et al. 1998).

Most marine macroscopic green algae investigated lack MAAs (references in Carreto and Carignan, 2011). Table 4 summarizes MAA composition in Chlorophyta macroalgae. Mycosporine-glycine and porphyra-334 are two MAA present in *Boodlea composita* and *Caulerpa racemosa* (reference in Carreto and Carignan, 2011) and also found in *Ulva lactuca* (sea lettuce) (Carefoot et al., 2000) with addicional shinorine and palythine. Gómez (1998) and coworkers found two unidentified MAA in *Dasycladus vermicularis* (M348 and M332). The algae *Prasiola crispa* subsp *antarctica* and *Prasiola stipitata* contained only M324 (reference in Carreto and Carignan, 2011; Gröniger and Häder, 2002) that was characterized as a putative MAA due to chromatographic properties (reference in Carreto and Carignan, 2011).

Table 2. MAAs identified in macroalgae *Rhodophyta* – Red seaweeds.

| Algae species | MAAs detected after UV exposure | References |
|---|---|---|
| *Acanthofora spicifera* | Porphyra-334, palythine, shinorine, palythinol, asterina-330; mycosporine-glycine | Carefoot et al. (2000) |
| *Asparagopsis taxiformis* | Unidentified MAAs | Sinha et al. (1998) |
| *Centrocerus clavulatum* | Shinorine, Asterina-330, Palythine, Palythinol (trace) | Carefoot et al. (2000) |
| *Chondrus crispus* | Shinorine, palythine, palythene, palythinol | Reference in Sinha et al. (1998) Sinha et al. (1998); Karsten et al. (1998) |
| *Condrus crispus* | Shinorine, palythine, asterina-330, palythinol, palyhene | Kräbs et al. (2002) |
| *Corallina elongata* | Shinorine, palythine | Sinha et al. (1998) |
| *Curdiea racovitzae* | Palythine, shinorine, palythinol | Reference in Sinha et al. (1998) |
| *Cystoclonium purpureum* | Shinorine, porphyra-334 | Sinha et al. (1998) |
| *Dumontia incrassata* | Shinorine, porphyra-334, palythine, mycosporine-gly | Sinha et al. (1998) |
| *Gelidium sp* | Shinorine | Sinha et al. (1998) |
| *Gracilaria chinensis* | Porphyra-334 (70%), shinorine (17-21%), palythine (5-10%), asterine-330 (5-10%) | Gómez et al. (2005) |
| *Gracilaria cornea* | Shinorine, porphyra-334 | Sinha et al. (2000) |
| *Gracilaria lemaneiformis* | M-265 nm | Xu and Gao (2010) |
| *Heterosigma akashiwo* | M-337 | Gao et al. (2007) |
| *Hydropuntia cornea* | Shinorine, porphyra-334, palythine | |
| *Iridaea chordata* | Palythine, shinorine, palythinol, palythene | References in Sinha et al. (1998) |
| *Jania rubens* | Shinorine, palythine, porphyra-334 | Sinha et al. (1998) |
| *Laurentia sp.* | Porphyra-334, Palythine, Asterian-330, Shinorine, mycosporine-glycine, Palythinol | Carefoot et al. (2000) |
| *Lithothamnion cf. antarcticum* | Shinorine, porphyra-334 | Reference in Sinha et al. (1998) |
| *Palmaria decipiens* | Palythine, palythene, porphyra-334, palythinol, shinorine | Reference in Sinha et al. (1998) |
| *Palmaria decipiens* | Shinorine, porphyra-334, palythine, asterina-330, palythinol, palythene, usujirene, M-335/360 | References in Carreto and Carignan (2011) |
| *Palmaria palmata* | Palythine, shinorine, asterina-330, palythinol, porphyra-334, usujirene | Yuan et al. (2009) |
| *Palmaria palmata* | mycosporine-glycine, shinorine, porphyra-334, palythine, asterina-330, palythinol and palythene, M-357 | Karsten and Wiencke (1999) |
| *Phyllophora antarctica* | Shinorine, palythene | Reference in Sinha et al. (1998) |
| *Phyllophora appendiculata* | Shinorine | Reference in Sinha et al. (1998) |
| *Porphyra sp.* | Porphyra-334, shinorine | Figueroa et al. (2003) |
| *Porphyra leucosticta* | Porphyra-334, palythine and asterina-330 and shinorine | Korbee et al. (2005) |
| *Porphyra umbilicalis* | Shinorine, porphyra-334 | Sinha et al. (1998) |
| *Pseudolithophyllum expansum* | Shinorine, porphyra-334 | Sinha et al. (1998) |

Table 3. MAAs identified in macroalgae Phaeophyceae – Brown seaweeds.

| Algae species | MAAs detected after UV exposure | References |
|---|---|---|
| | *Phaeophyceae* – Brown seaweeds | |
| *Ascophyllum nodosum* | Shinorine, porphyra-334 | Sinha et al. (1998) |
| *Desmarestia aculeata* | Shinorine, porphyra-334 | Sinha et al. (1998) |
| *Fucus spiralis* | Shinorine | Sinha et al. (1998) |
| *Padina crassa* | Shinorine, porphyra-334 | Reference in Sinha et al. (1998) |

Table 4. MAAs identified in macroalgae *Chlorophyta* – Green seaweeds.

| Algae species | MAAs detected after UV exposure | References |
|---|---|---|
| *Boodlea composita* | Mycosporine-glycine, porphyra-334 | Reference in Carreto and Carignan (2011) |
| *Caulerpa racemosa* | Mycosporine-glycine, porphyra-334 | Reference in Carreto and Carignan (2011) |
| *Cladophora rupestris* | Shinorine, porphyra-334, palythine | Sinha et al. (1998) |
| *Codium fragile* | Palythine, porphyra-334 | Reference in Sinha et al. (1998) |
| *Dasycladus vermicularis* | M-348, M-332 | Gómez et al. (1998) |
| *Enteromorpha intestinalis* | Unknown MAAs | Sinha et al. (1998) |
| *Prasiola crispa subsp antarctica* | M-324 | Reference in Carreto and Carignan (2011) |
| *Prasiola stipitata* | M-324 | Gröniger and Häder (2002) |
| *Ulva lactuca* | Mycosporine-glycine, shinorine, Porphyra-334, Palythine | Carefoot et al. (2000) |

**Seagrasses**

Seagrasses and submerged aquatic plants are subject to the influence of UV-B radiation due to the penetration of harmful UV-B wavelengths to considerable depths as forementioned.

The potential for aquatic plants to minimize UV-damage needs more investigation. However, varying degrees of response to increased UV radiation were found in seagrasses. Seagrasses *Halophila ovalis* and *Halodule uninervis* showed little UV-blocking response, exhibiting large decrease in photosynthetic efficiency and chloroplast density, showing a low resistance in UV exposure (reference in Short and Neckles, 1999). On the other hand, *Zostera capricorni*, *Cymodocea serrulata* and *Syringodium isoetifolium* were more UV tolerant due to the production of blocking pigments. Increases in UV-B radiation cause increases in plant content of phenolic and other secondary compounds (including flavonoids), which in turn, may increase the plant's resistance to herbivores and pathogens as well as decrease rates of decomposition (reference in Short and Neckles, 1999).

**Scitonemin**

Scitonemin is a yellow-brown lipid soluble pigment located in the extracellular polysaccharide sheath of some cyanobacteria (references in Singh et al., 2010b). Nägeli first reported it in 1849 but Proteau and coworkers (1993) identified its chemical structure in 1993. Scitonemin is a dimer composed of indolic and phenolic subunits having a molecular mass of 544 Da (Singh et al., 2010b), with a maximum wavelength of 250 nm. The linkage between two subunits in this pigment is an olefinic carbon atom that is unique among natural products (Singh et al., 2010b).

The Raman spectrum of the photoprotective pigment Scytonemin (C36H20N2O4) with the chemical name of 3,3'-bis-(4-hydroxybenzylidene)-3H,3'H-<1,1'>bi<cyclopenta<*b*>indolyl>-2,2'-dione found in cyanobacteria was obtained for the first time by Edwards et al. (1999).

Scitonemin is thought to be synthesized from metabolites of aromatic amino acids biosynthesis under high photon fluence rate (reference in Singh et al., 2010b). This pigment was isolated for the first time in an intertidal *Lyngbya* (cyanobacteria) (Edwards et al., 1999). Experimental evidence showed that both increase in temperature and oxidative stress in combination with UV-A, have a synergistic effect on high production of scytonemin (Singh et al., 2010b). This pigment is exclusively of cyanobacteria.

**Antioxidant compounds**

UV- radiation induces a general rise in activities of various antioxidant enzymes such as superoxide dismutase (SOD), peroxidase (POX), catalase (CAT) and glutathione reductase (GR) (Mallick and Mohm, 2000; Wang et al., 2007),

ascorbate-peroxidase (APX), dehydroascorbate reductase (DHAR) and monodehydroascorbate reductase (MD-HAR) to counteract oxidative stress (Li et al., 2010). In plants, the generated $O_2^{\cdot-}$ can beconverted into $H_2O_2$ and $O_2$ by several SOD isoenzymes: mitochondrial manganese SOD (Mn-SOD), chloroplast iron SOD (Fe-SOD) and cytosolic copper and zinc SOD (Cu/Zn SOD) (reference in Li et al., 2010). CAT and POX efficiently catalyse the breakdown of $H_2O_2$. APX is another powerful $H_2O_2$ scavenging enzyme, which utilizes AsA to eliminate the toxic product $H_2O_2$ by the oxidation of AsA to the monodehydroascorbate (MDHA) (reference in Li et al., 2010). APX isoenzymes are distributed in at least four distinct cellular compartments, including stromal APX (sAPX), thylakoid membrane-bound APX (tAPX) in chloroplasts, microbody membrane-bound APX (mAPX) and cytosolic APX (cAPX) (reference in Li et al., 2010). There is significant evidence showing that algae exposed to oxidative stress tend to increase the activities of ROS scavenging enzymes (references in Li et al., 2010). This indicates, as referred by Li et al. (2010), that higher and more stable antioxidant enzyme activities, either constitutive or induced, are associated with a higher stress tolerance in algae. Studies conducted by Aguilera et al. (2002), as referred by Li et al. (2010), comparing antioxidant enzyme activities among twenty-two macroalgae species (five green, seven red and ten brown) to UV radiation, showed that algal tolerance to oxidative stress was correlated with an enhancement of oxygen-reactive scavenging system. Li et al. (2010) evaluated the performance of SOD, POX, CAT and APX activities and isomorphs which catabolized $O_2^{\cdot-}$ and hydrogen peroxide in *Coralina officinalis* L. (Rhodophyta), to further identify the biochemically relevant pathways and protective mechanisms when exposed to UV-B. Results showed that superoxide dimutase (SOD) and peroxidase (POX) increased and then maintained at a relatively stable level when subjected to UV-B irradiation. Catalase (CAT) activity under medium dosage of UV-B irradiation (Muv) and high dosage of UV-B irradiation (Huv) treatments were significantly decreased. Ascorbate peroxidase (APX) activity first remained unaltered and then increased in Huv treatment. The activities of some SOD isoforms were altered by UV-B. Two new bands (POX V and POX VII) appeared upon exposure to all three UV-B dosages. CAT III activity was increased by low dosage of UV-B irradiation (Luv), whereas CAT III and CAT IV disappeared when the alga was exposed to Muv and Huv. Two bands of APX (APX VI and APX VII) were increased and a new band (APX X) was observed under Huv exposure. $H_2O_2$ and thiobarbituric acid reacting substance (TBARS) increased under Muv and Huv treatments. Overall, UV-B protection mechanisms are partly inducible and to a certain extent sufficient to prevent the accumulation of damage in *C. officinalis*. The antioxidant defense mechanism against ROS is pivotal for algal survival under stressful conditions (references in Li et al., 2010).

The intertidal macroalga *Hypnea musciformis*, showed a photoprotective adaptation strategy against UV-B damage, an increase of 58.9% phenolic compounds and 3.6% of carotenoids (Schmidt et al., 2012). *P. umbilicalis* (Sampath-Wiley et al., 2008) exhibited increased antioxidant metabolism, which could contribute to its success in colonizing stressful habitats like intertidal shores. In contrast, *Arthrospira (Spirulina) platensis*, showed accumulation of ROS by the presence of high levels of UVR, inhibited the activities of superoxide dismutase (SOD) and catalase (CAT) to cope with UVR (Ma and Gao, 2010).

Non-enzymatic components such as GSH (reduced glutathione), ascorbic acid, α-tocoferol, β-carotene, flavonoids, hydroquinones, among others, following exposure to UV radiation (Mallick and Mohm, 2000) have been reported and seems to be evident. Cellular thiols, especially glutathione, appear to play a key role in protection against oxidative damage arising from a number of stress conditions (Malanga et al., 1999). The role of N-acetylcysteine (NAC) as a protector against oxidative damage associated with ultraviolet in the microalga *Chlorella vulgaris* cultures was evaluated by Malanga et al. (1999). Treatments with NAC kept ascorbyl and lipid radical content in algae exposed to UV-B. Supplementation with 1mM NAC did not affect the content of lipid-soluble antioxidants (α-tocopherol, β-carotene) in algae cells (Malanga et al., 1999).

Phenolic extracts from the macroalgae *Macrocystis pyrifera* and *Porphyra columbina* exhibited high photoprotective activity, close to complete photoprotection (100%) (Guinea et al., 2012).

A comparative study with the brown seaweed *Pelvetia canaliculata* and the marine angiosperm *Salicornia ramosissima* (purple glasswort), two marine macrophytes growing in the upper intertidal zone, was conducted by Hupel et al (2011). This study showed that high doses of UV-B radiation induced few changes in carotenoid contents for

both species, suggesting efficient constitutive contents for photoprotection. This study also showed a fast acclimation of the brown seaweed, since both phenols and carotenoids related to a strong antioxidant protection. *S. ramosissima* showed a slow acclimation with a putative down regulation of phenols and the preferential involvement of carotenoids and/or other photoprotective systems.

**Heat shock proteins**

Heat shock proteins (HSPs) are synthesized by living cells as a response to stressful conditions, such as exposure to elevated temperatures, xenobiotics, heavy metals, free radicals, and UVR (Dahms and Lee, 2010). Among known heat shock proteins, only *hsp70* has been studied in marine ectotherms exposed to UVR. *Hsp 70* was suggested Matranga et al. (2006) (as referred by Dahms and Lee, 2010) to be a sensitive indicator of UV-B stress, as it is established by Bonaventura et al. (2006) (as referred by Dahms and Lee, 2010) a dose-dependent increase in *hsp70* protein levels in embryos of the sea urchin *Paracentrotus lividus* (Lamarck) exposed to UV-B doses. *Hsp70* had been identified in some microalgae: 46 species of cyanobacteria in six species of green algae (Chlorophyta) and in the diatoms *Thalassiosira pseudomana* and *Phaeodactylum tricornutum*. In algae, *hsp70* can help to acclimate to the environment (eg *Chlamydomonas* sp.) and adjust asymmetric divisions (*Volvox carteri*) (references in Zhang et al., 2011), or contribute to repairing photosystem II damage in *Dunaliella salina*. Fu et al. (2011) working with *Ulva pertusa* found a correlation between transcriptions and stress induction in this alga species and held that *hsp70* played an important role in the stresses. In the green seaweed *Ulva (Enteromorpha) prolifera*, the transcription of *hsp70* was up-regulated by UV irradiation, heat treatment and salinities induction, and less influenced by desiccation (Zhang et al., 2011). The authors suggest the use of *hsp70* in prediction of stress tolerance in algae and as a potential bio-indicator to monitor the stresses in seawater environments in the future.

**Other UV absorbing compounds**

The physiological responses of the aquatic liverwort *Jungermannia exsertifolia* sups. *cordifolia* were analyzed by Arróniz-Crespo and coworkers (2008) especially considering the UV radiation-induced responses of five hydroxycinnamic acid derivatives. This bryophyte lives in mountain streams, exposed to low temperatures and high UV levels (Arróniz-Crespo et al., 2008). This combination, high UV and low temperature, increase the adverse effects of UV. Arróniz-Crespo et al. (2008) and Fabón et al. (2012) found this liverwort species to have a dynamic protection and acclimation capacity to the irraciance and spectral characteristics of the radiation received. Studies conducted by Arróniz-Crespo et al. (2008) proposed three of the five UV-absorbing hydroxycinnamic acid derivatives as bioindicators of enhanced UV radiation: *p*-coumaroylmalic acid, 5”-(7”,8”-dihydroxycoumaroyl)-2-caffeoylmalic acid and 5”-(7”,8”-dihydroxy-7-*O*-β-glucosyl)-2-caffeoylmalic acid.

**DNA repair**

The most studied DNA repair process involves pyrimidine dimers repairing. The most common type of DNA damage induced by UVR is the formation of cyclobutyl pyrimidine dimmers (CPDs) and pyrimidine (6-4) pyrimidone photoproducts, leading to mutagenic, teratogenic or lethal effects in organisms, because these lesions prevent DNA replication and transcription. Organisms use different types of DNA repair mechanisms including photoenzymatic repair (PER), nucleotid excision repair (NER) and post-replication repair (Vincent and Roy, 1993).

Photoenzymatic repair (photoreactivation) (PER), is used to reverse cyclobutane dimers in DNA. It relies on the enzymatic activity and energy of photolyase at UV and visible light wavelengths (reference in Dahms and Lee, 2010). This DNA repair mechanism is widely distributed in nature and photoreactivation has been found in members of all kingdoms, although it is apparently lacking in several species or groups such as mammals (reference in Dahms and Lee, 2010).

Nucleotic excision repair (NER) is a more complex repair process that requires damage recognition, incision of the DNA strand near the site of the lesion, the excision and resynthesis of the DNA around the damaged site, and finally, ligation of the single strand after the DNA polymerase detaches (reference in Dahms and Lee, 2010). NER appears to be universally distributed though it is not thought to be very efficient at repairing CPDs (Dahms and Lee, 2010).

**UVR combined effects and ecological impacts**

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 are 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.

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). 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.

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

Effects of UV radiation are complex because organisms face different stressors.

The increase of UVR absorbing pigments is a primary defence mechanism against UVR damage, since their presence reduces plankton organism's transparency in the UVR. This increases its sighting distance for predators and prey with UV vision. This presents a dilemma for transparent epipelagic zooplankton that either needs to protect itself by sunscreen or to maintain its camouflage strategy in order to prevent predation. This conflict is particularly difficult to resolve in clear, oceanic waters where UVR levels are high.

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

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 finfish aquaculture industry.

**Conclusions**

A large body of information is available about UVR photobiology, particularly since the awareness of ozone depletion. Yet, long terms consequences of UVR exposure on organisms and what consequence in the ecosystems balance are 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).

The sensitivity of organisms to UVR has been shown to relate to differences in the efficiency of their protective mechanisms and repair systems (Dahms and Lee, 2010). A better understanding of such mechanisms will allow the development of technologies to monitor and address the adverse impacts of UVR (Dahms and Lee, 2010).

Details of the pathway and the enzymes involved in the biosynthesis, transference, accumulation and transformations of more than 20 fully characterized MAAs and of the recently discovered compounds, are still unknown and further studies are required. Nevertheless, there are biochemical evidences to assume that the high diversity of MAAs present in marine organisms is mainly derived from the synthesis and transformation of the so-called "primary MAAs". (Carreto and Carignan, 2011). In addition to the ecological significance of MAAs as sun-screening substances, these compounds have potential applications in cosmetics and toiletries as a UV protectors and activators of cell proliferation with therapeutic properties that may be exploited in a large amount of commercial applications (Carreto and Carignan, 2011).

Most of the scientific work available is based on laboratory tests exposing a single species and using artificial UV light to produce unrealistic environmental conditions, providing little useful information, because interspecific interactions, self-protective behaviour and chemical interactions with naturally occurring organic matter are not accounted for. It is critical to identify interactions between multiple stressors and UVR, because the combined effects are turning out to be astonishingly complex and could include abiotic interactions in addition to biodegradation and bioactivation of chemicals by UVR.

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 context 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).

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