Chapter 20
Impacts of Stratospheric Ozone Depletion and Solar UVB Radiation on Seaweeds

Kai Bischof and Franciska S. Steinhoff

20.1 Introduction

Reports on the thinning of the stratospheric ozone (O_3) layer in the early 1980s resulted in intense research activities aiming to assess and predict effects of an increased ultraviolet-B (UVB) radiation on biological systems, human skin, physiological key processes, e.g., photosynthesis, plant development, animal performance as well as terrestrial and marine ecosystem structure. Despite recent reports on the recovery of the Antarctic ozone hole (Newman et al. 2009; Kerr 2011), the impact of UVB on humans is still regarded as one of the most striking health issues in areas close to the Antarctic convergence (e.g., New Zealand, Southern Chile, Southern Argentina). Over the Arctic, however, the less stable atmospheric conditions result in extreme interannual variation in O_3 concentration, with a record loss in stratospheric O_3 being reported in spring 2011 (see press release by the European Space Agency (ESA) http://www.esa.int/esaCP/SEMIF24SZLG_index_0.html). Therefore, serious concern about the impacts of high UVB radiation on the biosphere still drives significant research efforts in the Polar regions of both hemispheres, based on the calculation that a 10% decline in column ozone would result in an approximately 5% increase of surface irradiance at 320 nm while the same decline would be accompanied by a 100% increase at 300 nm (Frederick et al. 1989), thus in the harmful range of UVB radiation. Among scientists there is large consensus about the success of the Montreal protocol, which

---

K. Bischof (✉)
Department of Marine Botany, Bremen Marine Ecology, University of Bremen,
Leobener Str. NW2, 28359 Bremen, Germany
e-mail: kbischof@uni-bremen.de

F.S. Steinhoff
Department of Biological and Environmental Sciences, University of Gothenburg, P.O. Box 461
40530 Göteborg, Sweden
e-mail: Franciska.Steinhoff@ntnu.no

C. Wiencke and K. Bischof (eds.), *Seaweed Biology*, Ecological Studies 219,
DOI 10.1007/978-3-642-28451-9_20, © Springer-Verlag Berlin Heidelberg 2012

was signed in 1987 with the intention to minimize emission of O_3-depleting CFCs (chlorofluorocarbons), and thus ozone depletion might be further slowed down in the future. However, due to the inertia of the atmosphere, recovery of the ozone layer may still not be observed for the next two decades. Furthermore, there is large uncertainty on how ozone depletion will interact with other aspects of climate change, e.g., the greenhouse effect (UNEP 2010). These interactions will be crucial also to the future radiation climate on the earth's surface.

In general, the effects of UVB exposure on biological systems are manifold, primarily acting on the molecular level, but with the potential to reach out to changes in ecosystem structure and function. The prerequisite for UVB-induced damage is its absorption by any kind of biomolecule. UV-chromophores in plants include nucleic acids (such as DNA, RNA) and proteins (Vass 1997). The results of UVB absorption by DNA are structural alterations like the formation of cyclobutane dimers, single-strand breaks, and pyrimidine (6–4)-pyrimidone (6–4)-photoproducts (Lois and Buchanan 1994). Furthermore, DNA damage may indirectly be induced by free oxygen radicals, generated by the electron transfer from chromophore molecules, excited by UVR absorption (Mitchell and Karentz 1993). UVB-mediated damage to proteins includes the splitting of disulfide bonds, which are crucial for protein folding, and thus, are essential for its proper functioning (Vass 1997). In algae, pigments of the photosynthetic apparatus are critical targets of UVR (Strid et al. 1990), with the phycobilins being highly sensitive, and carotenoids being less affected than chlorophylls (Häder and Häder 1989). The UVB-mediated damage to molecular targets may directly perpetuate with central physiological processes like, e.g., photosynthesis (Strid et al. 1990; Bischof et al. 2006a; see Chap. 1 by Hanelt and Figueroa) and nutrient uptake (Flores-Moya et al. 1998; Gómez et al. 1998). These physiological effects may also be reflected by changes on the ultrastructural level like, e.g., by the formation of "inside-out" vesicles from thylakoids, which was demonstrated in some red algal species (Poppe et al. 2002, 2003). Evidently, the impairment of physiological processes may further result in impairment of growth, production, and reproduction and may thus also alter ecosystem function (Han 1996a, b; Makarov 1999; Aguilera et al. 1999; Altamirano et al. 2000a, b).

Due to their crucial importance to coastal ecosystem function, seaweeds became a prominent group of organisms in UVB research. This chapter focuses on ecophysiological/autecological UV responses found in seaweeds, for further information on synecological implications like, e.g., interspecific competition and trophic interactions the reader is referred to the review by Bischof et al. (2006a). From the number of studies on UVB effects on seaweeds conducted so far, some general patterns can be concluded:

1. The species-dependent susceptibility of the alga involved is strongly correlated with the vertical zonation pattern the alga displays in the field. Moreover, even algal material, which is in culture for several years revealed that there is a genetically fixed adaptation and differential UVB susceptibility reflecting the UVB climate of the original distribution patterns (both vertical and latitudinal) of the species (Bischof et al. 1998a, b).

2. Within one species, juvenile and smaller specimens are generally more vulnerable than adult and larger algae. The reproductive microstages are more susceptible than adult sporophytes and acclimation to UVB exposure is possible, to at least some extent, for most of the species investigated so far (Dring et al. 1996; Roleda et al. 2007).
3. Phylogenetically old organismic groups, like algae, have evolved under conditions with much higher UVB irradiances in the atmosphere than nowadays, even under conditions of severe ozone depletion. Thus, most organisms have developed some kind of strategies to cope with the adverse effects of UVB exposure, which can be summarized by the terms: avoidance, protection, and repair (see Bischof et al. 2006a).
4. UVR may also confer promoting effects, like, e.g., the induction of photorepair processes (Hanelt and Roleda 2009).

20.2 Species-Dependent UV Susceptibility Based on Latitudinal and Depth Distribution: The Frame Set by Adaptation

The frame of species-dependent reactions of seaweeds to UVB exposure is set by genetically fixed adaptation. Early laboratory studies on Antarctic seaweeds, which were kept in stock cultures for more than 10 years still revealed distinct species-specific reaction patterns toward UV exposure once they were grown to macrothalli and exposed to identical UV conditions (Bischof et al. 1998a). Thus, it was confirmed that shallow water species, like the two green algae *Enteromorpha bulbosa* (now termed *Ulva bulbosa,* also referred to as *U. hookeriana*) and *Acrosiphonia arcta,* were still extremely UV tolerant even after long-term exposure to dim light conditions in stock cultures. In contrast, photosynthesis of the red algal species, *Phycodrys austrogeorgica* and *Delesseria lancifolia,* responded extremely sensitive toward UV exposure. Overall, the general zonation patterns seaweeds display, e.g., at the islands off the Antarctic Peninsula are reflected by their UV sensitivity even decades after their isolation from the field (Bischof et al. 1998a).

The same adaptational setting has been observed in six red algal species from cold-temperate regions and with different zonation patterns with respect to their species-specific growth rates and ability to cope with UVB-mediated DNA damage (van de Poll et al. 2001). Again, these algae were cultivated under identical culture conditions and exposed to similar irradiance of UVB and, evidently, the respective inhibition of growth was in line with the species position on the shore, with the two shallow water species (*Palmaria palmata* and *Chondrus crispus*) hardly exhibiting inhibition in growth, whereas in deep-water algae (*Phycodrys rubens* and *Polyneura hilliae)* growth was inhibited almost completely. Furthermore, accumulation of damaged DNA, expressed as thymine dimer formation, was found in the two deep-water species, which apparently lack the ability for sufficient DNA repair. This confirms the strong adaptation of these species to their low irradiance environment at their natural growth site. Furthermore, the accumulation of DNA damage in seaweeds can be regarded as a very good measure for the degree of adaptation of a given species towards UVB exposure (van de Poll et al. 2001).

These findings were also confirmed in a transplantation experiment on another deep-water red algal species *Delesseria sanguinea*, in which growth was also impaired when the alga was exposed to surface solar radiation (Pang et al. 2001). Results obtained indicated the absence of any protecting mechanisms against excessive radiation in this algal species, which are, however, not relevant to the species as it inhabits the low light environments in the shade of canopy algae or in great water depths. Thus, sublittoral seaweeds may avoid being exposed to UVB simply by growing in water depths, in which most of the UVB irradiance is already attenuated by the water column above. A prominent example of this avoidance strategy is also the Arctic endemic deep-water kelp *Laminaria solidungula* (Brey 2009). Other algal species following this strategy may also be growing in the understory being protected by the algae above or following a cryptic life cycle.

Generally, all modulation of ecophysiological reactions toward variation in abiotic factors is conditioned by genetic adaptation. This is also visible in two red algal species from Spitsbergen (Arctic) with slightly different vertical zonation preferences (Karsten et al. 1999): *Devaleraea ramentacea* as a species from shallow waters is permanently equipped with high activities of reactive oxygen scavenging superoxide dismutase (SOD, see Chap. 6 by Bischof and Rautenberger). This high but static activity is reasonable for a species from shallow waters, where usually strong variation in abiotic conditions and, thus, the onset of stressful conditions to photosynthesis potentially resulting in increased ROS production is more likely than in more stable deeper waters. However, maintaining a protective system on such a high level throughout the year is probably energetically cost intense. Thus, species which are not permanently exposed to stressful conditions, e.g., in deeper waters, may favor the strategy to rather respond to abiotic stress and to increase protective strategies, like SOD activity, only when they are needed during times of, e.g., high UV irradiance. *Palmaria palmata* inhabiting slightly deeper waters than *D. ramentacea* is applying this strategy (Karsten et al. 1999; see also Bischof et al. 2006a).

20.3 Acclimation to UV Exposure in Space and Time: Depth Distribution, Small-Scale Gradients, and Season

Seaweeds populating a flexible environment, i.e., the shallow water zones, coastlines with strong seasonality, etc., require mechanisms of acclimation in order to set physiological performance to the variation of environmental requirements. Thus, also acclimation toward UV exposure has been widely observed in seaweeds. Acclimation of photosynthesis to UV exposure has been demonstrated in the Arctic/cold-temperate kelp *Alaria esculenta* from Spitsbergen

(Bischof et al. 1999; see also Chap. 1 by Hanelt and Figueroa). The potential for acclimation is not only the precondition to endure stress caused by exposure to harmful radiation, but is a prerequisite to establish over wide depth ranges and to endure the seasonal variation of radiation conditions (Bischof et al. 1998b, 1999). However, the process of acclimation of photosynthetic activity in Arctic brown seaweeds to changing radiation conditions showed a distinct sequence of events, which may be indicative for the different molecular mechanisms involved: in *A. esculenta* under repeated UV exposure, the competence of recovery from UV-induced photoinhibition increased after just a few exposure/recovery cycles. This might indicate an activation of different repair mechanisms, counteracting the impact of UV exposure by a faster replacement of damaged molecules. Moreover, the degree of inhibition became smaller (Bischof et al. 1998b, 1999), which might also be related to an activated ROS defense system counteracting UVB-mediated oxidative stress (see Chap. 6 by Bischof and Rautenberger) or to the formation of UV-screening compounds, like phlorotannins (Schoenwaelder 2002a, b).

In fact, biosynthesis and accumulation of UV-screening substances has been described as one of the most important physiochemical acclimation mechanisms against biologically harmful UV radiation. In red algae, mycosporine-like amino acids (MAAs) have been extensively studied as potent UV-screening substances (Karsten et al. 1998; Conde et al. 2000). While MAAs have been mainly observed in the Rhodophyta (Hoyer et al. 2001; Huovinen et al. 2004), Phaeophyta and most Chlorophyta typically lack these compounds, with the green alga *Prasiola crispa* ssp. *antarctica* being an interesting exception and containing high concentrations of a unique MAA with an absorption maximum at 324 nm (Hoyer et al. 2001; Karsten et al. 2005). The role of MAA accumulation as an acclimatory response toward the respective radiation environment becomes apparent from the observed decrease in cellular concentration with increasing depth (Hoyer et al. 2001). In general, cellular MAA concentrations in red algae have been shown to be positively correlated with the natural UV doses (Karsten et al. 1998; Huovinen et al. 2004). The flexibility of acclimation with respect to the synthesis of UV-screening compounds is reflected by strong seasonal as well as microscale variation in MAA contents: thus, specimens of the red alga *Palmaria decipiens* collected in Antarctic winter contained low concentrations of UV-absorbing compounds and exhibited significantly higher values in summer (Post and Larkum 1993). Furthermore, in individual red algal specimens cross-sectional and longitudinal MAA concentration gradients have been described depending on the respective microenvironment of radiation, the age, or the tissue type (Karsten and Wiencke 1999; Hoyer et al. 2001). Based on their ability and flexibility of MAA synthesis, red algae have been classified into three categories (Hoyer et al. 2001): Type I—species which completely lack the ability to synthesize MAAs, as e.g., most of the deep-water algae; Type II—species which synthesize MAAs in variable concentrations in response to the variation of the respective environmental conditions, and Type III—species which always contain high concentrations of MAAs, typically these are algal species populating very shallow waters or even the intertidal zone and are, thus, exposed to strong irradiances and large amplitudes of environmental variation.

Similar traits of optical protection against UVB exposure can also be found in brown seaweeds, however, based on another class of chemical compounds, the so-called phlorotannins (Ragan and Glombitza 1986). Phlorotannins have been invoked as multifunctional compounds acting in deterring herbivores and microbes, in adhesion and in strengthening algal cell walls (Schoenwaelder 2002b), and in absorbing UV radiation (Ragan and Glombitza 1986; Pavia et al. 1997; Henry and Van Alstyne 2004). Phlorotannins do also possess a high antioxidant activity (e.g., Ahn et al. 2007) and are, thus, important for scavenging ROS. With respect to the acclimation of brown seaweeds toward exposure to detrimental UV radiation several strategies have been described in which phlorotannins do play a vital role: (1) a generally high tissue concentration of phlorotannins acting as UV screen (Schoenwaelder 2002a, b), (2) an induction of phlorotannins in response to the environmental radiation conditions (Halm et al. 2010), (3) an exudation of phlorotannins and other phenolic compounds into the surrounding medium creating an UV-absorbing microenvironment (Pérez-Rodríguez et al. 1998; Roleda et al. 2010; Steinhoff et al. 2011b), or (4) an excess inclusion of phlorotannins in cell walls shielding harmful radiation (Schoenwaelder 2002b). An induction of phlorotannins after exposure to UVB radiation was first described in the brown alga *Ascophyllum nodosum* (Pavia et al. 1997). An induction of phlorotannins due to UVB and UVA radiation was also described for *Macrocycstis integrifolia* (Swanson and Druehl 2002). An increase in the size of phlorotannin containing vesicles, the so-called physodes, was observed in various Laminariales from Spitsbergen after UVB exposure indicating an induction of phlorotannin synthesis (Wiencke et al. 2006). This has recently been verified in the UV-tolerant species *Alaria esculenta* and *Saccorhiza dermatodea* (Steinhoff unpublished data, Steinhoff et al. 2011b). An exudation of phlorotannins as response to artificial UVB radiation was observed in *Macrocystis integrifolia* (Swanson and Druehl 2002) creating so-called UV-refugia. Again, high phlorotannin contents and high exudation rates might reflect an adaptation of seaweeds to the radiation climate and overall habitat requirements. In contrast, induction and variable exudation rates of phlorotannins reflect the acclimation potential to environmental changes. Interestingly, the precursors of MAAs and phlorotannins are both synthesized by the Shikimate pathway, with phenylalanine being an important intermediate. The reason why finally different specific UV screens are applied in different algal divisions represents an interesting aspect to study in terms of algal evolution.

In contrast to the specific UV-absorbing compounds found in red and brown algae, there is inconsistency about the role of optical UV protection in the group of green algae. The occurrence of MAAs in supralittoral green algae such as *Prasiola* sp. (Karsten et al. 2005) seems to be quite exceptional. Similar as phlorotannin exudation in brown algae, some green seaweeds have also been found to generate microenvironments depleted from UVB, e.g., by excreting UVB-absorbing substances. The green *Dasycladus vermicularis* is commonly found in the shallow waters of the Mediterranean as well as in rock pools. Under conditions of high irradiance and increased water temperature and salinity, the alga excretes high concentration of hydroxycumarine, a phenolic compound which may provide a yellowish color to the water body around and thus may increase UVB absorption in the water, before it may reach algal specimens (Pérez-Rodríguez et al. 1998, 2001). However, an extended screening of 71 green macroalgal species revealed that in fact optical UV screening in green seaweeds is rather exceptional (Pescheck et al. 2010), and thus green algae largely need to rely on alternative mechanisms to resist the harmful effects of UV exposure. An alternative strategy to achieve optical shielding on a cellular base is the arrangement of specimens in dense assemblages, e.g., macroalgal mats. In these systems which are usually formed by highly opportunistic species (e.g., *Ulva, Chaetomorpha*) under high nutrient loads and low wave exposure, physiologically healthy and productive algal material is shielded by the algal layers above, generating a steep small-scale gradient of UVB and PAR, but also chlorophyll content and photosynthetic performance in those assemblages (Bischof et al. 2002, 2006b). A prominent example for the effectiveness of this strategy is found in mats of *Ulva rotundata* from southern Spain (Bischof et al. 2002, 2003). Thus, this protection by canopy arrangement does not require the synthesis of specific UV-screening compounds; however, it is at the expense of the top algal layers.

20.4 Interaction with Other Abiotic Factors

Seaweeds and particularly those inhabiting the intertidal and shallow subtidal are exposed to (inter-) dependently changing abiotic parameters; thus the interactive effects of UV radiation in concert with the change of other abiotic parameters are important to address. In the early studies on UV effects on seaweed physiology conducted under laboratory conditions, the proper ratio of radiative power of the different wavelength ranges was largely neglected and the significance to the effects observed was largely underestimated. Among others, this was shown in a study conducted on the green macroalga *Ulva lactuca* isolated from Greenland (Fredersdorf and Bischof 2007). Here algal material was exposed to a constant irradiance of UVB radiation, however, at different irradiances of background photosynthetically active radiation (PAR). The different effects on algal photosynthesis of the respective wavelengths ranges (PAR, UVA, UVB) were identified by the combination of various cutoff filters. In this study, the importance of background PAR for the impact of UVB effects observed became evident: The extent of UVB-induced inhibition of photosynthetic quantum yield was highly dependent on the irradiance of PAR in the setup and was diminishing with increasing PAR irradiance. However, due to the different mechanisms of PAR- and UVB-induced inhibition of photosynthesis, the additional effect of UVB rather became apparent in the recovery kinetics from photoinhibition, resulting in a delay of recovery under UVB exposure, presumably due to the increased defragmentation of photosynthetic units, i.e., the D1 reaction centre protein. In contrast, increased levels of PAR as well as UVA may provide an additional energy input to fuel simultaneously operating repair processes counteracting the damaging impact of UV exposure, e.g., by an increased activity of DNA photolyase, or elevated expression of psbA-gene and consequently enhanced turnover of D1. Therefore, the ecological implications of UVB exposure can only be validated in approaches mimicking natural radiation conditions, particularly reflecting the naturally occurring relative ratios of the different wavelength ranges. In particular, algae and aquatic plants from high irradiance environments (e.g., tropical shallow water ecosystems) show distinct (sometimes even promoting) interactions of UVB- and PAR-induced photoinhibition (Hanelt et al. 2006; Hanelt and Roleda 2009).

The importance of temperature for the respective UV susceptibility observed in seaweeds has also been demonstrated; however, the level of knowledge is still far behind compared to that existing for higher plants, in which, e.g., a chilling-induced increase in optical UV screening has been observed, even in the absence of UVB (Bilger et al. 2007). This observation formed the base for intense studies on the interactive effects of temperature and UVB exposure. Low temperatures generally pose the problem of slowed down enzyme reactions and consequently generally reduced metabolic activity. *In concreto*, this also applies to enzymatic repair processes in response to UVB exposure. At low temperatures, the activity of repair enzymes (DNA-photolyase, excision repair), as well as synthetic pathways (e.g., D1-turnover) might be not operative at the velocity required to keep up with rate of damage occurring at a certain irradiance (of UVB and/or PAR); thus, accumulation of damage will be the consequence. In turn, under conditions of reduced activity of repair enzymes, organisms may rely more strongly on optical protection strategies. However, studies on the photoprotective potential of phlorotannins in Arctic brown algal zoospores and juvenile gametophytes revealed that changes in phlorotannin content were neither affected by low nor by high temperatures (Müller et al. 2009; Steinhoff et al. unpublished). Taking the high antioxidative potential of phlorotannins (Connan et al. 2006; Zubia et al. 2007) into consideration, phlorotannins might be produced and rapidly oxidized again (Steinhoff et al. 2012). Therefore, photoprotective substances might also help to protect brown macroalgal cells by scavenging ROS within a wide temperature range. Nevertheless, several studies investigating the interactive effects of temperature and UV exposure on macroalgal spores (Wiencke et al. 2006; Müller et al. 2008, 2009; Steinhoff et al. 2011a, b) lead to the conclusion that at low temperatures, solar radiation effects might be better compensated than at increased water temperatures indicating the potential impact of rising water temperatures on early macroalgal life stages.

Still, a moderately increased temperature has been found to compensate for UVB-induced damage due to the higher activity of repair pathways. The impact of temperature increase on UV susceptibility of photosynthetic activity was studied in two *Ulva* species from Antarctic and subantarctic regions (Rautenberger and Bischof 2006). An isolate of the Antarctic/cold-temperate *Ulva bulbosa* (now also referred to as *U. hookeriana*) was compared to the cosmopolitan *U. clathrata* by exposing them to identical conditions of UV radiation at 0° and 10°C. In both species, exposure to 10°C almost completely compensated for the UV-induced inhibition of photosynthetic quantum yield observed at 0°C (see Fig. 20.1). Observed results were striking for two reasons: (1) in *U. bulbosa* UV-induced

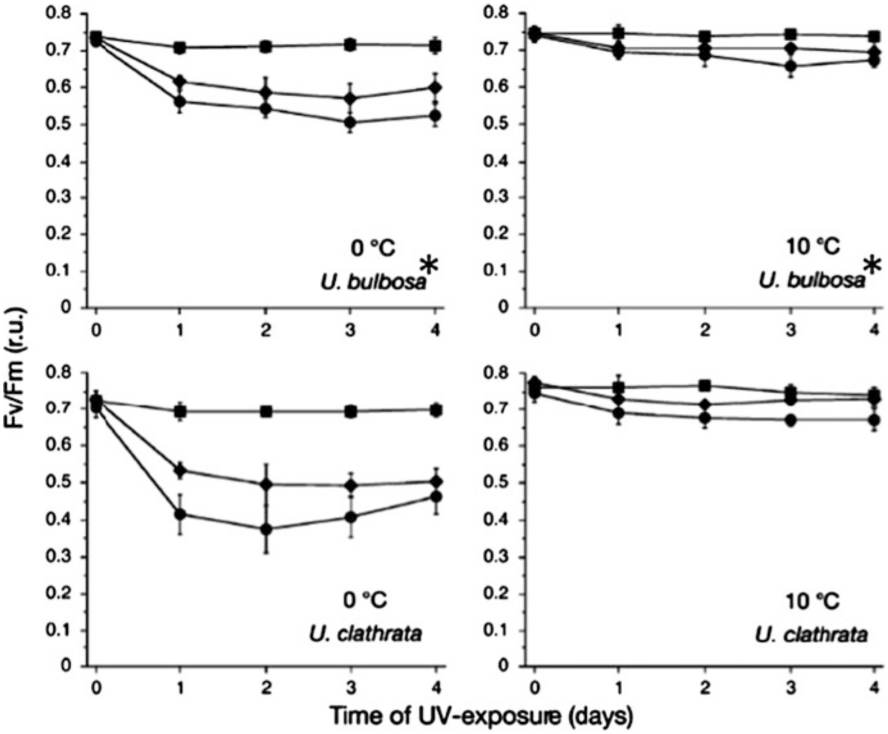

Fig. 20.1 Interactive effects of UV exposure and temperature on optimum quantum yield of photosynthesis (F_v/F_m): *Ulva bulbosa,* (*now also referred to as *U. hookeriana*) (isolated from King George Island, Antarctica) and *U. clathrata* (isolated from Puerto Williams, Tierra del Fuego, South America) have been exposed to identical irradiances of PAR, UVA, and UVB at 0° and 10°C; (*filled square*) PAR alone, (*filled diamond*) PAR + UVA, (*filled circle*) PAR + UVA + UVB (Rautenberger and Bischof 2006)

inhibition was compensated by temperatures, which are higher than those usually encountered at its natural growth sites; (2) in the cosmopolitan species *U. clathrata* exposure to lower temperatures resulted in strongly pronounced UV effects, even stronger than in the more southern species *U. bulbosa*, which might be based on higher SOD activities measured in the latter species, presumably as a result of higher cellular SOD concentrations. It has been described as a common adaptive feature in Polar organisms to increase respective enzyme concentrations in order to compensate for activity loss at low environmental temperatures. However, temperature compensation of UV effects is evidently only possible within the temperature tolerance range of the species under investigation.

A further aspect of environmental change has raised new concerns on marine ecosystem functions and resulted in further research activities with respect to the potential impacts of ocean acidification (see Chap. 19 by Roleda and Hurd). Hitherto, there is very little information available on how the impacts of UV radiation and changing pH levels might interact with respect to seaweed physiology. Currently, only one pilot study has been conducted on the calcifying red alga *Corallina sessilis* indicating some synergistic effects of UV- and low pH-exposure on growth, photosynthetic oxygen evolution, and calcification (Gao and Zheng 2010). Revealing synergisms of both environmental factors on a wider range of marine organisms will be an important research direction, which needs to come up in the very near future.

20.5 UV Effects on Different Life History Stages and Implications for Reproduction and Recruitment

In recent years, UV research on seaweeds focused particularly on the potential impacts of climate change, ozone depletion, and UVB exposure on the microscopic reproductive stage. It has been shown for a number of the ecologically most important species of kelp (order Laminariales and related) that the sensitivity toward UVB radiation is highly dependent on the respective life history stage under investigation (Dring et al. 1996; Wiencke et al. 2006; Roleda et al. 2007; Müller et al. 2008). Generally, the unicellular zoospores of kelps have been identified as the developmental stage most vulnerable toward UVB exposure (Wiencke et al. 2000). This is amongst others based on the small sizes of spores and thus large surface-to-volume ratios, which facilitate the penetration of harmful radiation into the cell and thus the damage to cellular components. Another explanation for the high UVB susceptibility of spores is provided by the level of ploidy. With respect to zoospores and gametes being haploid stages, UVB-mediated damage to the DNA bears even more severe consequences, as single copy genes might be damaged without a potential substitute by a second allele, as e.g., in the diploid sporophytes (Roleda et al. 2008). Evidently, the impact of UVB exposure on the reproductive success of seaweeds is determined by the most UVB susceptible stage in the life history of a species. There is common sense that if there will be an adverse impact of UVB radiation on seaweed communities it will be mediated by a disruption of the developmental cycle due to pronounced damage to the haploid, unicellular life history stages (zoospores and gametes), which will ultimately preclude reproduction and recruitment (Roleda et al. 2007; Müller et al. 2008, 2009; Steinhoff et al. 2011b).

Via its significance to the reproductive microstages, impacts of solar UV radiation on the cellular level are closely related to effects on a community level as it may result in, e.g., impaired release of zoospores (Makarov and Voskoboinikov 2001) and recruitment (Wiencke et al. 2000, 2006; Roleda et al. 2007). At present, only a small number of publications describe UVR effects on cellular ultrastructure of seaweed spores (Steinhoff et al. 2008). UV effects observed on the ultrastructural level include wrinkled thylakoid membranes, dilatations of the thylakoid lumen, and disrupted mitochondria with plastoglobuli formation as well as changes of the nucleoplasm structure (Poppe et al. 2002, 2003; Holzinger et al. 2004; Holzinger and Lütz 2006; Steinhoff et al. 2008; see also Karsten et al. 2009).

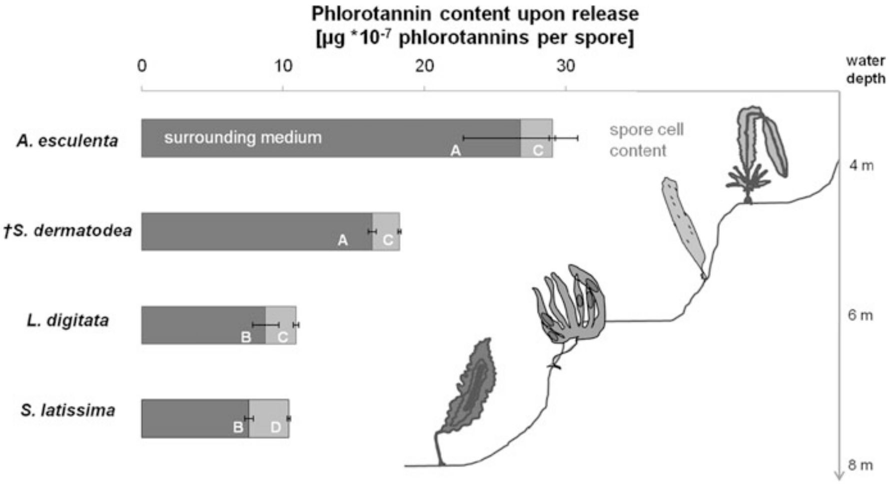

Fig. 20.2 Collection depth of *Alaria esculenta, Saccorhiza dermatodea* [†data from Steinhoff et al. (2011b)], *Laminaria digitata,* and *Saccharina latissima* from Kongsfjorden, Spitsbergen in correlation with the sum of phlorotannin content [µg × 10^{-7} phlorotannin spore^{-1}] within the surrounding medium and the zoospores. Vertical zonation of sublittoral Arctic brown algae species reflects parental phlorotannin content liberated upon spore release. *Capital letters* indicate statistical differences ($p < 0.05$) and vertical bars standard deviation ($n = 3$). Steinhoff et al. previously unpublished

Consequently, cellular protection against harmful UVB is particularly vital for the microscopic reproductive stages of seaweeds. Studies on brown algal spores under elevated radiation scenarios suggest that phlorotannins are highly variable due to inter- and intraspecific variations (Toth et al. 2005; Connan et al. 2006), developmental stage (van Alstyne et al. 2001), habitat (Hemmi and Jormalainen 2004), and season (Plouguerné et al. 2006). Likewise are the multiple roles and tasks of phlorotannins within different species and their developmental stages very likely to be determined by interaction of a variety of biotic and abiotic factors (Pavia et al. 1997). The vertical zonation pattern of the parental algae seems to be coupled with the amount of exuded phlorotannins, with high amounts of released phlorotannins in species and specimens from the upper sublittoral compared to individuals from the lower sublittoral (Fig. 20.2, Steinhoff et al. unpublished, Wiencke et al. 2006). The induction of phlorotannins (Pavia et al. 1997) is most likely time dependent; a significant phlorotannin formation at mid-term scales (i.e., 10 days) within macroalgal juveniles of *S. latissima* and *A. esculenta* (Steinhoff et al. 2011a) could be detected while it is lacking on short-term (i.e., 8 h) scales (Müller et al. 2009; Steinhoff et al. 2011b). Parental efforts and the respective conditioning of parental seaweeds toward the respective UV exposure at the natural growth site seem to play a major role to increase viability of the offspring by "transferring" the acquired UVR tolerances to their reproductive stages (Steinhoff et al. 2011b).

Again, not only the isolated effects of UV exposure should be considered: Short-term exposure of macroalgal propagules to high PAR revealed the underestimation of PAR effects compared to UVR. While adult macroalgae are able to cope with higher irradiation due to more developed adaptive/acclimation processes, high PAR seems to have a more detrimental impact on spore germination and total fatty acid content and composition than assumed before (Steinhoff et al. 2011a; Steinhoff et al. 2012). With respect to future scenarios for seaweed ecosystem functions under elevated temperatures and UVB irradiances, high PAR should be studied as an interactive parameter for all life history stages.

20.5.1 Synthesis

This chapter focused largely on autecological responses of seaweeds under UVB exposure. However, species-specific responses ultimately result in significant ecological implications, which include changes in distributional patterns (latitude vs. depth distribution), succession patterns, and species diversity, and may further result in altered biotic relationships, e.g., competition and trophic interactions (see Bischof et al. 2006a for review), which are, however, beyond the scope of this chapter. Taking into account the multitude of effects UVB exerts on the physiology and ecology of a species, it is apparent that UVB exposure plays indeed an important role in shaping seaweed-dominated coastal ecosystems. Based on the knowledge acquired so far it might be concluded that in line with the respective growth site, physiological activity of most seaweeds is sufficiently buffered and thus protected against increasing UVB. However, this assumption still neglects the importance of the interaction with other abiotic and biotic factors to be expected to change under future environmental perturbations. Still most data on UV impacts on seaweeds available so far have been obtained from laboratory experiments: Studies under more realistic environmental conditions are still needed. In particular, mesocosm approaches under natural irradiation and experimental variation of temperature and pH should be designed to obtain a better understanding of organismic interaction (e.g., changes in benthic/shallow water food web structure) in an era of climate change (Zacher et al. 2007).

References

Aguilera J, Karsten U, Lippert H, Vögele B, Philipp E, Hanelt D, Wiencke C (1999) Effects of solar radiation on growth, photosynthesis and respiration of macroalgae from the Arctic. Mar Ecol Prog Ser 19:109–119

Ahn GN, Kim KN, Cha SH, Song CB, Lee J, Heo MS, Yeo IK, Lee NH, Jee YH, Kim JS, Heu MS, Jeon YJ (2007) Antioxidant activities of phlorotannins purified from *Ecklonia cava* on free radical scavenging using ESR and H_2O_2-mediated DNA damage. Eur Food Res Technol 226:71–79

Altamirano M, Flores-Moya A, Figueroa FL (2000a) Long-term effects of natural sunlight under various ultraviolet radiation conditions on growth and photosynthesis of intertidal *Ulva rigida* (Chlorophyceae) cultivated in situ. Bot Mar 43:119–126

Altamirano M, Flores-Moya A, Figueroa FL (2000b) Growth seasonality, photosynthetic pigments, and C and N content in relation to environmental factors: a field study on *Ulva olivascens* (Ulvales, Chlorophyta). Phycologia 39:50–58

Bilger W, Rolland M, Nybakken L (2007) UV screening in higher plants induced by low temperature in the absence of UV-B radiation. Photochem Photobiol Sci 6:190–195

Bischof K, Hanelt D, Wiencke C (1998a) UV-radiation can affect depth-zonation of Antarctic macroalgae. Mar Biol 131:597–605

Bischof K, Hanelt D, Tüg H, Karsten U, Brouwer PEM, Wiencke C (1998b) Acclimation of brown algal photosynthesis to ultraviolet radiation in Arctic coastal waters (Spitsbergen, Norway). Polar Biol 20:388–395

Bischof K, Hanelt D, Wiencke C (1999) Acclimation of maximal quantum yield of photosynthesis in the brown alga *Alaria esculenta* under high light and UV radiation. Plant Biol 1:435–444

Bischof K, Peralta G, Kräbs G, van de Poll WH, Perez-Llorens JL, Breeman AM (2002) Effects of solar UV-B radiation on canopy structure of *Ulva* communities from Southern Spain. J Exp Bot 53:2411–2421

Bischof K, Janknegt PJ, Buma AGJ, Rijstenbil JW, Peralta G, Breeman AM (2003) Oxidative stress and enzymatic scavenging of superoxide radicals induced by solar UV-B radiation in *Ulva* canopies from southern Spain. Sci Mar 67:353–359

Bischof K, Gomez I, Molis M, Hanelt D, Karsten U, Lüder U, Roleda MY, Zacher K, Wiencke C (2006a) Ultraviolet radiation shapes seaweed communities. Rev Environ Sci Biotechnol 5:141–166

Bischof K, Rautenberger R, Brey L, Perez-Llorens JL (2006b) Physiological acclimation along gradients of solar irradiance within mats of the filamentous green macroalga *Chaetomorpha linum* from southern Spain. Mar Ecol Prog Ser 306:165–175

Brey L (2009) Acclimation of kelp photosynthesis to seasonal changes in the underwater radiation regime of an Arctic fjord system. PhD thesis, Universität Bremen, pp 98

Conde FR, Churio MS, Previtali CM (2000) The photoprotector mechanism of mycosporine-like amino acids. Excited-state properties and photostability of porphyra-334 in aqueous solution. J Photochem Photobiol 56B:139–144

Connan S, Delisle F, Deslandes E, Gall EA (2006) Intra-thallus phlorotannin content and antioxidant activity in Phaeophyceae of temperate waters. Bot Mar 49:39–46

Dring MJ, Makarov V, Schoschina E, Lorenz M, Lüning K (1996) Influence of ultraviolet-radiation on chlorophyll fluorescence and growth in different life history stages of three species of *Laminaria*. Mar Biol 126:183–191

Flores-Moya A, Gomez I, Vinegla B, Altamirano M, Perez-Rodriguez E, Maestr C, Caballero RM, Figerueroa FL (1998) Effects of solar radiation on the endemic Mediterranean red alga *Rissoella verruculosa*: photosynthetic performance, pigment content and the activities of enzymes related to nutrient uptake. New Phytol 139:673–683

Frederick JE, Snell HE, Haywood EK (1989) Solar ultraviolet radiation at the earth's surface. Photochem Photobiol 50:443–450

Fredersdorf J, Bischof K (2007) Irradiance of photosynthetically active radiation determines UV-susceptibility of photosynthesis in *Ulva lactuca* L. (Chlorophyta). Phycol Res 55:295–301

Gao K, Zheng Y (2010) Combined effects of ocean acidification and solar UV radiation on photosynthesis, growth, pigmentation and calcification of the coralline alga *Corallina sessilis* (Rhodophyta). Global Change Biol 16:2388–2398

Gómez I, Pérez-Rodríguez E, Viñegla B, Figueroa FL, Karsten U (1998) Effects of solar radiation on photosynthesis, UV-absorbing compounds and enzyme activities of the green alga *Dasycladus vermicularis* from southern Spain. J Photochem Photobiol B Biol 47:46–57

Häder DP, Häder M (1989) Effects of solar and artificial radiation on motility and pigmentation in *Cyanophora paradoxa*. Arch Microbiol 152:453–457

Halm H, Lüder UH, Wiencke C (2010) Induction of phlorotannins through mechanical wounding and radiation conditions in the brown macroalga *Laminaria hyperborea*. Eur J Phycol 46:16–26

Han T (1996a) Effect of ultraviolet-B radiation on *Ulva pertusa* Kjellman (Chlorophyta) I Growth and pigment content. Algae (Kor J Phycol) 11:155–159

Han T (1996b) Far-UV action on growth, pigmentation and photosynthesis of *Ulva lactuca* (Chlorophyta). Algae (Kor J Phycol) 11:203–206

Hanelt D, Roleda MY (2009) UVB radiation may ameliorate photoinhibition in specific shallow-water tropical marine macrophytes. Aquat Bot 91:6–12

Hanelt D, Hawes I, Rae R (2006) Reduction of UV-B radiation causes an enhancement of photoinhibition in high light stressed aquatic plants from New Zealand lakes. J Photochem Photobiol B Biol 84:89–102

Hemmi A, Jormalainen V (2004) Geographic covariation of chemical quality of the host alga *Fucus vesiculosus* with fitness of the herbivorous isopod *Idotea baltica*. Mar Biol 145:759–768

Henry BE, van Alstyne KL (2004) Effects of UV radiation on growth and phlorotannins in *Fucus gardneri* (Phaeophyceae) juveniles and embryos. J Phycol 40:527–533

Holzinger A, Lütz C (2006) Algae and UV irradiation: effects on ultrastructure and related metabolic functions. Micron 37:190–207

Holzinger A, Lütz C, Karsten U, Wiencke C (2004) The effect of ultraviolet radiation on ultrastructure and photosynthesis in the red macroalgae *Palmaria palmata* and *Odonthalia dentata* from Arctic waters. Plant Biol 6:568–577

Hoyer K, Karsten U, Sawall T, Wiencke C (2001) Photoprotective substances in Antarctic macroalgae and their variation with respect to depth distribution, different tissues and developmental stages. Mar Ecol Prog Ser 211:117–129

Huovinen P, Gómez I, Figueroa FL, Ulloa N, Morales V, Lovengreen C (2004) Ultraviolet-absorbing mycosporine-like amino acids in red macroalgae from Chile. Bot Mar 47:21–29

Karsten U, Wiencke C (1999) Factors controlling the formation of UV-absorbing mycosporine-like amino acids in the marine red alga Palmaria palmata from Spitsbergen (Norway). J Plant Physiol 155:407–415

Karsten U, Sawall T, Hanelt D, Bischof K, Figueroa FL, Flores-Moya A, Wiencke C (1998) An inventory of UV-absorbing mycosporine-like amino acids in macroalgae from polar to warm-temperate regions. Bot Mar 41:443–453

Karsten U, Bischof K, Hanelt D, Tüg H, Wiencke C (1999) The effect of UV-radiation on photosynthesis and UV-absorbing substances in the endemic Arctic macroalga *Devaleraea ramentacea* (Rhodophyta). Physiol Plant 105:58–66

Karsten U, Friedl T, Schumann R, Hoyer K, Lembcke S (2005) Mycosporine-like amino acids (MAAs) and phylogenies in green algae: *Prasiola* and its relatives from the Trebouxiophyceae (Chlorophyta). J Phycol 41:557–566

Karsten U, Wulff A, Roleda MY, Müller R, Steinhoff FS, Fredersdorf J, Wiencke C (2009) Physiological responses of polar benthic algae to ultraviolet radiation. Bot Mar 52:639–654

Kerr RA (2011) First detection of ozone hole recovery claimed. Science 332(6026):160

Lois R, Buchanan BBN (1994) Severe sensitivity to ulraviolet radiation in an *Arabidopsis* mutant deficient in flavonoid accumulation: II. Mechanisms of UV-resistance in Arabidopsis. Planta 194:504–509

Makarov M (1999) Influence of ultraviolet radiation on the growth of the dominant macroalgae of the Barents Sea. Chemosphere Global Change Sci 1:461–467

Makarov MV, Voskoboinikov GM (2001) The influence of ultraviolet-B radiation on spore release and growth of the kelp *Laminaria saccharina*. Bot Mar 44:89–94

Mitchell DL, Karentz D (1993) The induction and repair of DNA photodamage in the environment. In: Young AR, Björn LO, Moan J, Nultsch W (eds) Environmental UV photobiology. Plenum, New York, pp 345–377

Müller R, Wiencke C, Bischof K (2008) Interactive effects of UV radiation and temperature on microstages of Laminariales (Phaeophyceae) from the Arctic and North Sea. Clim Res 37:203–213

Müller R, Wiencke C, Bischof K, Krock B (2009) Zoospores of three Laminariales under different UV radiation and temperature conditions: Exceptional spectral absorbance properties and lack of phlorotannin induction. Photobiol Photochem 85:970–977

Newman PA, Nash ER, Douglass AR, Nielsen JE, Stolarski RS (2009) Estimating when the Antarctic ozone hole will recover. In: Zerefos C, Contopoulos G, Skalkeas G (eds) Twenty years of ozone decline. Springer, Berlin, pp 191–200

Pang S, Gómez I, Lüning K (2001) The red macroalga *Delesseria sanguinea* as a UVB-sensitive model organism: selective growth reduction by UVB in outdoor experiments and rapid recording of growth rate during and after pulses. Eur J Phycol 36:216–297

Pavia H, Cervin G, Lindgren A, Åberg P (1997) Effects of UV-B radiation and simulated herbivory on phlorotannins in the brown alga *Ascophyllum nodosum*. Mar Ecol Prog Ser 157:139–146

Pérez-Rodríguez E, Gómez I, Karsten U, Figueroa FL (1998) Effects of UV radiation on photosynthesis and excretion of UV-absorbing compounds of *Dasycladus vermicularis* (Dasycladales, Chlorophyta) from southern Spain. Phycologia 37:379–387

Pérez-Rodríguez E, Aguilera J, Gómez I, Figueroa FL (2001) Excretion of coumarins by the Mediterranean green alga Dasycladus vermicularis in response to environmental stress. Mar Biol 139:633–639

Pescheck F, Bischof K, Bilger W (2010) Screening of UV-A and UV-B radiation in marine green macroalgae (Chlorophyta). J Phycol 46:444–455

Plouguerné E, Le Lann K, Connan S, Jechoux G, Deslandes E, Stiger-Pouvreau V (2006) Spatial and seasonal variation in density, reproductive status, length and phenolic content of the invasive brown macroalga *Sargassum muticum* (Yendo) Fensholt along the coast of Western Brittany (France). Aquat Bot 85:344–377

Poppe F, Hanelt D, Wiencke C (2002) Changes in ultrastructure, photosynthetic activity and pigments in the Antarctic red alga *Palmaria decipiens* during acclimation to UV radiation. Bot Mar 45:253–261

Poppe F, Schmidt RAM, Hanelt D, Wiencke C (2003) Effects of UV radiation on the ultrastructure of several red algae. Phycol Res 51:11–19

Post A, Larkum AW (1993) UV-absorbing pigments, photosynthesis and UV exposure in Antarctica: comparision of terrestrial and marine algae. Aquat Bot 45:231–243

Ragan MA and Glombitza KW (1986) In: Round FE and Chapman DJ (eds) Phlorotannins, brown algal polyphenols. Prog Phycol Res 4:129–241

Rautenberger R, Bischof K (2006) Impact of temperature on UV susceptibility of two species of *Ulva* (Chlorophyta) from Antarctic and Subantarctic regions. Polar Biol 29:988–996

Roleda MY, Wiencke C, Hanelt D, Bischof K (2007) Sensitivity of the early life stages of macroalgae to ultraviolet radiation. Photochem Photobiol 83:851–862

Roleda MY, Zacher K, Wulff A, Hanelt D, Wiencke C (2008) Susceptibility of spores of different ploidy levels from Antarctic Gigartina skottsbergii (Gigartinales, Rhodophyta) to ultraviolet radiation. Phycologia 47:361–370

Roleda MY, Lüder UH, Wiencke C (2010) UV-susceptibility of zoospores of the brown macroalga *Laminaria digitata* from Spitsbergen. Polar Biol 33:577–588

Schoenwaelder MEA (2002a) Physode distribution and the effects of "Thallus Sunburn"in *Hormosira banksii* (Fucales, Phaeophyceae). Bot Mar 45:262–266

Schoenwaelder MEA (2002b) The occurence and cellular significance of physodes in brown algae. Phycologia 41:125–139

Steinhoff FS, Wiencke C, Müller R, Bischof K (2008) Effects of ultraviolet radiation and temperature on the ultrastructure of zoospores of the brown macroalga *Laminaria hyperborea*. Plant Biol 10:388–397

Steinhoff FS, Graeve M, Wiencke C, Wulff A, Bischof K (2011a) Lipid content and fatty acid consumption in zoospores/developing gametophytes of *Saccharina latissima* (Laminariales, Phaeophyceae) as potential precursors for secondary metabolites as phlorotannins. Polar Biol 34(7):1011–1018

Steinhoff FS, Wiencke C, Wuttke S, Bischof K (2011b) Effects of enhanced water temperatures, UV radiation and low versus high PAR on phlorotannin content and germination in zoospores of *Saccorhiza dermatodea* (Tilopteridales, Phaeophyceae). Phycologia 50(3):256–263

Steinhoff FS, Graeve M, Bischof K, Wiencke C (2012) Phlorotannin production and lipid oxidation as a potential protective function against high photosynthetically active and UV radiation in gametophytes of *Alaria esculenta* (Alariales, Phaeophyceae). Photochem Photobiol 88(1): 46–57

Strid A, Chow WS, Anderson JM (1990) Effects of supplementary ultraviolet-B radiation on photosynthesis in *Pisum sativum*. Biochim Biophys Acta 1020:260–268

Swanson AK, Druehl LD (2002) Induction, exudation and the UV protective role of kelp phlorotannins. Aquat Bot 73:241–253

Toth GB, Langhamer O, Pavia H (2005) Inducible and constitutive defenses of valuable seaweed tissues: consequences for herbivore fitness. Ecology 86:612–618

UNEP 2010 Annual Report, United Nations Environment Programme, pp 124

van Alstyne KL, Whitman SL, Ehlig JM (2001) Differences in herbivore preferences, phlorotannin production, and nutritional quality between juvenile and adult tissues from marine brown algae. Mar Biol 139:201–210

van de Poll WH, Eggert A, Buma AGJ, Breeman AM (2001) Effects of UV-B-induced DNA damage and photoinhibition on growth of temperate marine red macrophytes: habitat-related differences in UV-B tolerance. J Phycol 37:30–37

Vass I (1997) Adverse effects of UV-B light on the structure and function of the photosynthetic apparatus. In: Pessarakli M (ed) Handbook of photosynthesis. Marcel Dekker, New York, pp 931–949

Wiencke C, Gómez I, Pakker H, Flores-Moya A, Altamirano M, Hanelt D, Bischof K, Figueroa FL (2000) Impact of UV-radiation on viability, photosynthetic characteristics and DNA of brown algal zoospores: implications for depth zonation. Mar Ecol Prog Ser 197:217–229

Wiencke C, Roleda M, Gruber A, Clayton M, Bischof K (2006) Susceptibility of zoospores to UV radiation determines upper depth distribution limit of Arctic kelps: evidence through field experiments. J Ecol 94:455–463

Zacher K, Wulff A, Molis M, Hanelt D, Wiencke C (2007) Ultraviolet radiation and consumer effects on a field-grown intertidal macroalgal assemblage in Antarctica. Global Change Biol 13:1201–1215

Zubia M, Robledo D, Freile-Pelegrin Y (2007) Antioxidant activities in tropical marine macroalgae from the Yucatan Peninsula, Mexico. J Appl Phycol 19:449–458