VIEW PAPER

Ultraviolet radiation shapes seaweed communities

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Abstract Stratospheric ozone depletion and the concomitant increase in irradiance of ultraviolet-B radiation (UVB) at the earth's surface represent major threats to terrestrial and aquatic ecosystems. In costal rocky shore environments, seaweeds constitute a group of organisms of particular significance to ecosystem function. Thus, impairment of seaweed performance by UVB-exposure may result in severe changes in the functioning of coastal ecosystems. Here we present our view on how UVB radiation affects seaweed physiology and ecology and, thus, shapes the coastal environment by affecting the spatial, species and functional structure of seaweed communities.

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Introduction to seaweed communities

Seaweeds (also referred to as "marine macroalgae") represent key components within coastal ecosystems (Lüning 1990). As primary producers these green, brown or red coloured marine plants serve a multitude of ecosystem functions. They may grow from just a few millimetres in size up to 60 m or even more. At their growth site they often form submersible forests (i.e., "kelp forests" in cold-temperate oceans) characterized by high primary productivity. For instance, along the coasts of cold-temperate regions, the communities dominated by the brown algal genus *Laminaria* have annual productivity rates of about 2 kg carbon per m^2 (Thomas 2002). Seaweeds are globally distributed from the Tropics to the Polar Regions and primarily settle on hard bottom substrate, such as rocky shorelines. Here, seaweed communities typically show distinct vertical zonation patterns exhibiting a characteristic sequence of

species with increasing depth (Stephenson and Stephenson 1972). Along with the depth gradient, the environmental parameters seaweeds are exposed to change drastically. Species settling in the supralittoral zone (the fringe above the high tide level) are exposed to drought, high solar radiation and also atmospheric changes in temperature. The intertidal fringe (the eulittoral zone) is moreover characterised by regular and extreme changes in abiotic conditions, based on tidal influence (Davison and Pearson 1996). During low tide, organisms are exposed to high solar irradiance, drought, atmospheric temperatures, and, depending on current weather conditions, sometimes extreme changes in salinity (Schonbeck and Norton 1978; Davison and Pearson 1996). Furthermore, mechanical stress due to tidal currents and wave exposure has a strong impact on intertidal communities. Underneath, in the sublittoral zone extending below the low tide level, seaweeds usually encounter a more stable habitat, as the water column above buffers against strong changes in abiotic parameters. As outlined below, it is also the respective characteristics of the water column, which determines exposure of sublittoral organisms towards UVB exposure.

Seaweeds interact with and play an existential role for many marine animals (Lubchenco and Gaines 1981; Hay and Fenical 1992). The most important functions of seaweeds in this context are the supply of food and habitat to and their effects on the recruitment and dispersal of animals. Being at the basis of marine food webs, seaweeds are directly consumed by a diversified suite of micro- and macrograzers, which in turn can alter structure and species composition of seaweed communities (Duffy and Hay 2000). In addition, algal exudates might fuel the microbial loop if they are used by free-living and alga-associated bacteria. However, algae can also adversely affect animals. For instance, decomposing algal mats produce anoxic conditions affecting survival of covered animals.

Seaweeds serve many species as habitat, to which sessile forms attach directly, and may host motile animals by provision of shelter from predators (Lippert et al. 2001). Open space is a key resource for sessile marine species and in this way, seaweeds ameliorate competition for space.

Seaweeds are also among the first multi-cellular colonizers and thus precondition the substratum for later successional recruits. Subsequent settlement of spores and larvae may be facilitated, tolerated, or inhibited in dependency of the already existing seaweed community (Sousa and Connell 1992). Furthermore, larger seaweeds serve as egg-deposition sites of predatory fin and shell fish, thereby supporting indirectly top-down control in coastal habitats. Furthermore, dislodged seaweeds serve as dispersal vectors for species, accelerating the transport of invasive species and the recolonisation of defaunated habitats (Thiel and Gutow 2005).

Due to their enormous importance within coastal ecosystems a decrease in seaweed abundance related to environmental change e.g., under increased UVB irradiance will thus have dramatic consequences for the sum of organisms associated. Even under the present radiation conditions, UVB represents a crucial environmental factor organisms have to deal with. The knowledge on the physiological and ecological effects of present UVB irradiances is a precondition in order to be able to estimate future consequences of ozone depletion and increased UVB levels. Thus, in the following we present our view on how UVB radiation may shape seaweed dominated coastal ecosystems under the present radiation conditions and how the spatial and functional structure of seaweed communities might be affected in the future.

Enhanced UVB radiation

Solar radiation is the most important prerequisite for life on earth. In the process of photosynthesis, photoautotrophic organisms (like seaweeds) convert light energy into chemically bound energy, which is used for biomass production; as a side effect, molecular oxygen is generated as a basis for all heterotrophic organisms. Changes in irradiance and light quality can either promote photosynthesis, but can also inhibit many biological processes if radiation becomes excessive (Barber and Andersson 1992), or if short wavelength radiation with high energy content, such as UVB radiation, is absorbed by

biomolecules (Vass 1997). Consequently, damage to important components in plant metabolism results in reduced photosynthetic and general metabolic activity and, hence, lead to a decrease in biomass production.

Ever since the discovery of stratospheric ozone depletion in the Antarctic in the 1970s (Farman et al. 1985), serious concerns have arisen about the impacts of increasing UVB radiation on the biosphere (Madronich et al. 1998; Björn et al. 1999). Ozone is predominantly generated in the low latitudes, by photolysis of molecular oxygen. In the stratosphere, ozone molecules are subject to UV-mediated photolysis and may also be degraded due to the reaction within catalytic cycles with NO, Cl or Br serving as catalysts (Lary 1997; Langer 1999). The concentration of these compounds in the atmosphere increases mainly due to anthropogenic emissions, thus leading to ozone depletion.

Ultraviolet radiation includes the wavelengths below those visible to the human eye. This spectral range is according to the CIE definition (Commission Internationale de l'Eclairage 1935) divided into three wavebands: 315–400 nm UVA, 280–315 nm UVB, and 190–280 nm UVC, which does not reach the earth's surface, as it is completely absorbed on its way through the atmosphere. Due to the optical characteristics of ozone, it is the UVB range, which is likely to increase at the earth's surface, as a consequence of a decrease in stratospheric ozone concentration. Calculations based on the absorption characteristics of O_3 indicate that a 10% decline in column ozone would result in an approx. 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).

UVB in the aquatic environment

The effects of UVB on aquatic ecosystems are strongly dependent on the optical properties of the water body (Holm-Hansen et al. 1993; Hanelt et al. 2001). Therefore, it is necessary to estimate the penetration of UV radiation into the water column. The UV irradiance reaching the water surface is influenced by various *atmospheric* factors, such as latitude and altitude, elevation of the sun coinciding to the season and the time of day, weather conditions (clouds and fog), ozone and aerosol concentrations. The *underwater* light field is even more variable: In coastal sea waters, UV radiation and blue light are strongly attenuated due to dissolved organic matter (DOM; Kirk 1994), and this depends largely on the input of this material from the terrestrial ecosystem. According to Kirk (1994), the diffuse vertical attenuation coefficient of downward irradiance (K_d) in the water column is determined by the following formula:

$$K_d = \ln(Ed_{(z_2)}/Ed_{(z_1)})^* (z_1 - z_2)^{-1}$$

with $Ed_{(z_1)}$ and $Ed_{(z_2)}$ as the respective irradiance in depth z_1 and z_2. The value of the K_d in the UV-waveband is naturally much higher than for the PAR range (Jerlov 1976) and typically increases tremendously during the summer season in polar coastal waters (Hanelt et al. 2001). The reason is that the turbidity of the coastal water in polar regions rises due to rainfall or melt water from snow layers and glaciers. A high discharge of turbid fresh water into the coastal zone carries fine terrigenous sediments into the seawater (Svendsen et al. 2002). In the Arctic the variation in K_d-values showed that from middle of June, UVB transparency decreased strongly due to the input of turbid melt waters on Spitsbergen (Hanelt et al. 2001) or in the Hudson bay (Vincent and Belzile 2003). While the UVB transmittance decreased only by about 22% per meter in clear waters during spring, the attenuation increased to about 53% per meter in summer, so that UVB was almost fully absorbed within the first 3 m of the water body at Spitsbergen. In spring and late autumn at low air temperatures the water conditions are relatively clear. Then, UV radiation penetrates deeply into the water column and the threshold irradiance of UVB with the potential to affect primary plant productivity negatively is still at about 5–6 m depth. In contrast to the situation in sheltered bays and fjords, at open coastlines with strong current, melt water can be replaced much faster with clearer oceanic water, which diminishes the observed turbidity effects on light penetration. Climate-induced changes in planktonic or

allochthonous sources of DOM, either through changes in vegetation cover, decomposition, or glacial meltwater may have a higher impact on the underwater UVB regime than ozone depletion would produce (Franklin et al. 2003). Vincent and Belzile (2003) found a close correlation between UV attenuation and seston concentration in the Antarctic region. In the south western Ross Sea a high particulate absorption in the UVB waveband was observed during a phytoplankton bloom which was rather caused by the absorption of chromophoric dissolved organic matter (Arrigo and Brown 1996). Arctic and Antarctic Oceans both experience increased biological UV exposure resulting from stratospheric ozone depletion. However, climate related sea ice melting in the Arctic may potentially result in greater change in underwater UVB exposure than the increase caused by recent ozone depletion in Antarctica (Vincent and Belzile 2003). In summary, the respective optical characteristics of the water column determine the under water light climate and thus also UVB absorption in the aquatic environment. As UVB exposure is decreasing with increasing depth, the attenuation of UV radiation in the water column represents a major structuring frame for seaweed communities.

Biological effects of UVB

The effects of UVB exposure on biological systems are manifold, and reach from the molecular to the organism level, thereby affecting growth and production, and, consequently, ecosystem structure and function. A prerequisite for UVB induced damage is the absorption by biomolecules. Potential UV-chromophores in plants mainly include nucleic acids (such as DNA, RNA) and proteins (Vass 1997). DNA is one of the most UV-sensitive molecules and UV-induced damage occurs directly by the absorption of UVB quanta by aromatic residues. The results are direct structural alterations such as formation of cyclobutane dimers (Lois and Buchanan 1994), but can also be indirectly mediated due to the presence of free oxygen radicals, generated by the electron transfer from chromophore molecules, excited by UV absorption (Mitchell and Karentz

1993). UV-induced damage to the DNA represents a serious effect, as photoproducts can inhibit replication or even cause mutations, thereby affecting gene expression. UVB absorbing aromatic residues are also present in certain amino acids (e.g., tyrosine, phenylalanine, tryptophan) and, therefore, in proteins. Consequently, damage to protein molecules is a major effect of UVB in organisms. Furthermore, disulphide bonds between cysteine residues in the protein can be cleaved by UVB radiation (Vass 1997). These bonds have an important role in protein folding, and thus, are essential for proper functioning of the protein. Lipids, a major compound in all biological membranes, may be destroyed by UVB in the presence of oxygen. This peroxidation of unsaturated fatty acids has a direct effect on membrane structure and the generation of lipid peroxy radicals can induce further damage by participating in free radical cascades (Murphy 1983). In plants, pigments of the photosynthetic apparatus can also be destroyed by UV exposure (Strid et al. 1990), with the phycobilins being the most sensitive, and carotenoids generally being less affected than the chlorophylls (Teramura 1983; Häder and Häder 1989). As a consequence of a number of molecular effects, several physiological processes are impaired, such as photosynthesis (Bornman 1989; Strid et al. 1990; Nogues and Baker 1995; Allen et al. 1997), and nutrient uptake (Döhler 1985, 1992; Flores-Moya et al. 1998; Gómez et al. 1998), while others, e.g., respiration, appear to be less affected (Larkum and Wood 1993; Aguilera et al. 1999).

Photosynthesis is probably the most intensively studied process in plant biology. Due to its central role in plant metabolism, as well as its importance for all oxygen dependent life on earth, studies on adverse effects on photosynthesis, in the context of a globally changing environment are of particular interest. Due to numerous effects of UVB radiation to the respective molecules involved in photosynthesis, the effects of UV-exposure are also multiple (see Vass 1997 for review). The common consequences on photosynthetic function are decreased CO_2-fixation and oxygen evolution (Renger et al. 1986; Allen et al. 1997). This could be caused by several molecular events: While most studies have found that photosystem I (PS I) is only

minimally affected by UVB (by inhibiting PS I-mediated cyclic photophosphorylation; Iwanzik et al. 1983; Renger et al. 1986), photosystem II (PS II) seems to be a more important target (Bornman 1989). It is likely that UVB causes an inhibition of energy transfer within the PS II reaction centre by blocking electron flow. Furthermore, the function of the D_1 protein may be impaired by the UVB induced fragmentation of the protein (Renger et al. 1986; Vass 1997). On the oxidising side of PS II, the oxygen evolving system (water splitting complex) is another sensitive target of UVB (Renger et al. 1986). Furthermore, it has been suggested that UVB may affect the light-harvesting complex (LHC) by its functional disconnection from the photosystem, resulting in an impairment of energy transfer to the reaction centre (Renger et al. 1986; Lorenz et al. 1997). A decrease in photosynthetic activity may also be due to the photodestruction of pigments; within the chlorophylls, Chl a has been observed to be more affected than Chl b (Teramura 1983; Strid et al. 1990).

The CO_2 fixing enzyme RubisCO has been shown to be another critical component in UVB-induced inhibition of photosynthesis. The UVB-induced decline in its activity is related to the decreasing amount of both subunits as well as the corresponding mRNA levels (Strid et al. 1990; Jordan et al. 1992; Bischof et al. 2000a, 2002a). Another effect of UVB on reactions related to photosynthesis represents the inactivation of chloroplast ATPase (Strid et al. 1990). Impairment of any of the components mentioned above contributes to lower the photosynthetic activity during and following UV-exposure.

The physiological effects are also reflected on the ultrastructural level. UVB radiation can lead to dramatic changes of the fine structure of chloroplasts and mitochondria. Mild UV stress leads to a wrinkled appearance of the thylakoids, lumen dilatations and damage of the outer membranes. In the mitochondria a swelling of the cristae is often observed (Poppe et al. 2003; Holzinger et al. 2004). After strong UVB exposure the formation of 'inside-out' vesicles from thylakoids was demonstrated in four red algal species. In *Palmaria decipiens* the fine structural changes are reversible indicating acclimation to UV stress (Poppe et al. 2002, 2003).

On the organism level, the effects mentioned above can result in reduced growth and production, as shown in higher plants, seaweeds, phytoplankton and ice algae (Caldwell 1971; Worrest 1983; Ekelund 1990; Karentz et al. 1991a, b; Holm-Hansen 1993; McMinn et al. 1999, Han 1996a, b; Makarov 1999; Aguilera et al. 2000; Altamirano et al. 2000a, b). Other effects include the impairment of reproductive success or may even bear lethal consequences. Consequently, all aspects mentioned may also affect ecosystem structures (Holm-Hansen et al. 1993; Johanson et al. 1995; Caldwell et al. 1998).

Seaweed responses to UVB

Seaweeds became a prominent group of organisms in UVB research for two reasons. Firstly, seaweeds represent a crucial component for coastal ecosystems. Thus, UVB related damage to these organisms might have drastic consequences to the entire ecosystem. Secondly, in a range of field and laboratory studies, seaweeds were proven to be in general rather sensitive to UVB exposure (at least compared to terrestrial plants) but also it was shown in some species growing over a wide depth or even geographical range, that seaweeds do apply a vast variety of acclimation mechanisms. Thus they became very suitable model systems also in basic stress physiology.

Adaptation versus acclimation

The respective reaction of a species towards UVB exposure is determined by the interplay of genetically fixed adaptation and physiological acclimation. Generally spoken, adaptation is setting the frame in which acclimation to changing environmental conditions might occur.

In a laboratory study on Antarctic seaweeds, which were isolated in the field decades ago and subsequently kept in stock cultures it was shown that these specimens still exhibit distinct species-specific differences in UV-tolerance once they are grown to macrothalli and exposed to identical culture and experimental UV conditions (Bischof et al. 1998a). Due to the cultivation of sporophytes under low-light conditions and UV-exclusion

no acclimation to UV radiation had occurred prior to the experiments. The two shallow-water green algae *Enteromorpha bulbosa* and *Acrosiphonia arcta* were least affected by UVB radiation. Photosynthesis in the brown algae *Desmarestia antarctica* and *D. anceps* and the red alga *Gymnogongrus antarcticus*, inhabiting slightly deeper waters, was inhibited to a similar and intermediate extent. However, two other red algal species from the lower subtidal, *Phycodrys austrogeorgica* and *Delesseria lancifolia*, responded extremely sensitively towards UVB-exposure. In the case of *Delesseria sanguinea*, a deep sublittoral species, growth can be also strongly impaired when the alga is exposed to surface solar radiation (Pang et al. 2001) indicating these plants may lack all protecting mechanisms against excessive radiation. In the field protective mechanisms against UV radiation might not be necessary because they live in the shade of the canopy algae and/or in great depths. Similarly, zoospores of the deep-water species *L. saccharina* and *L. hyperborea* are more strongly photoinhibited after exposure to UV radiation than zoospores from the shallow water species *L. digitata* (Roleda et al. 2005a). In addition, recovery of PS II activity is high in *L. digitata*, low in *L. saccharina* and lowest in *L. hyperborea*. Spores of the eulittoral *M. stellatus* and *C. crispus* are photoinhibited after UV exposure but recover quickly after exposure to dim white light (Bischof et al. 2000b; Roleda et al. 2004). The first attempt to study kinetics of photoinhibition and recovery in zoospores of Arctic Laminariales showed that zoospores of the lower sublittoral *L. saccharina* were more sensitive to PAR- and UV-induced photoinhibition than upper- to midsublittoral *S. dermatodea*, *A. esculenta* and *L. digitata*. Kinetics of recovery in zoospores showed a fast phase in *S. dermatodea* which indicates a reduction of the photoprotective process while a slow phase in *L. saccharina* indicates recovery from severe photodamage (Roleda et al. 2006d). These experiments were focussed on short-term effects, thus the preadaptive setting of species could be revealed, but not the respective potential of acclimation, also determined by the genetic features of species.

In another study, six different red algal species from cold-temperate regions and with different zonation patterns were cultivated under identical culture conditions and exposed to similar irradiance of UVB (van de Poll et al. 2001). The inhibition of growth became stronger in accordance with the position on the shore these algae usually take in the field. The two species from the upper sublittoral or even lower eulittoral zone (*Palmaria palmata* and *Chondrus crispus*) did hardly exhibit inhibition in growth, whereas growth in the species from the middle sublittoral zone (*Phyllophora pseudoceranoides* and *Rhodymenia pseudopalmata*) was inhibited up to 50%. In the deep-water algae *Phycodrys rubens* and *Polyneura hilliae*, growth was inhibited almost completely. Curiously, pronounced accumulation of damaged DNA, expressed as thymine dimer formation, was only found in these two species. Apparently these true deep-water algae do lack mechanisms to shield the DNA from UVB exposure or to repair already damaged DNA e.g., by the activity of repair-enzymes (as e.g., DNA phytolyase). This study illustrates how genetic pre-adaptation is setting the frame in which acclimation may occur. The fact that not any acclimation to UVB was shown by these species points to a strong degree of adaptation to low irradiance environments.

Modulation of ecophysiological reactions towards variation in abiotic factors is conditioned by genetic adaptation. This is also visible in two red algal species from Spitsbergen 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). 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 stressfull conditions to photosynthesis resulting in increased ROS production, is more likely than in more stable deeper waters. However, maintaining a protective systems on such a high level throughout the year is probably energetically costly. Thus, species which are not permanently exposed to stressfull conditions, e.g., in deeper waters, may favour the

strategy to 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). In the case of the estuarine red alga *Gracilaria chilensis*, which is subject to extremely changing light conditions both during tidal cycles and seasonally, exposures to surface UVB irradiances induce marked reductions in photosynthesis (Gómez et al. 2005a). Although the species can display rapid acclimation mechanisms, the constitutively high pigment contents and low concentrations of sunscreen substances (e.g., MAAs), clearly suggest that the *Gracilaria* retains its shade adapted characteristics, probably as a consequence of the normally turbid waters at the estuary.

Acclimation of photosynthesis to UV radiation

In seaweed species inhabiting a flexible environment, i.e., the shallow water zones down to approx. 15 m depth, acclimation to changing abiotic conditions is important, to adjust photosynthetic performance in order to maintain energy supply for growth, but also to prevail under periods of stressfull conditions. The ability for fast acclimation to increased UV irradiance has been demonstrated in the Arctic/cold-temperate kelp *Alaria esculenta* from Spitsbergen (Bischof et al. 1999). It was shown that its macrothalli are able to adjust photosynthetic performance to changes in irradiance at their respective growth site. This capability may represent one prerequisite for this species to establish over a wide depth range and also to endure the seasonal variation of radiation conditions (Chapman and Lindley 1980; Falkowski and LaRoche 1991; Klöser et al. 1996; Bischof et al. 1998b, 1999).

Within the brown algae studied so far, two different responses were observed in the process of acclimation of photosynthetic activity to changing radiation conditions. Firstly, the rate of recovery from UV-induced photoinhibition increases. Secondly, the degree of inhibition becomes smaller (Bischof et al. 1998b, 1999). Increases in the rate of recovery may result from an activation of different repair mechanisms, counteracting the impact of UV-exposure by a faster replacement of damaged molecules. The molecular mechanism responsible may be the same as discovered in the cyanobacteria *Synechocystis* sp. and *Synechococcus* sp. In both species, it was found that exposure to moderate doses of UVB results in an increased turnover rate of the D_1 and D_2 reaction centre subunits of PS II, thus, rapidly replacing damaged protein by newly synthesised polypeptides (Campbell et al. 1998; Máté et al. 1998). The latter authors found that UVB induces the transcription of psbA genes, which encode the D_1 reaction centre protein of PS II. Although comparable studies are lacking for macroalgae, it may be that a similar response provides an explanation for the increasing rate of recovery in the studied brown algal species. However, this mechanism may only be successful as long as UVB exposure does not induce stronger damage to DNA, thus impairing gene expression. Results also showed, that in algae previously acclimated to high PAR, additional UV-exposure rather results in a delay of the recovery process than in a further inhibition of photosynthesis (Bischof et al. 1999). These findings support data from field experiments on *Fucus distichus* from Spitsbergen, indicating that at their natural growth site in the eulittoral zone photoinhibition is mainly caused by high irradiances of PAR and natural UVB causing a delay in recovery (Hanelt et al. 1997a). The observed delay in recovery is indicative for damage to the D_1 protein (Aro et al. 1993). Under UVB exclusion the rate of D_1 degradation mediated by solar radiation was found to be as much as 30% slower than under full sunlight (Greenberg et al. 1989), thus supporting those results for high light acclimated algae.

In contrast to subtidal species, intertidal brown algae, have to cope with highly changing solar radiation scenarios on a short term basis. In this sense, high PAR irradiances become as ecological important as UV radiation. Flores-Moya et al. (1999) observed a significant delay in recovery from photoinhibition in the brown alga *Dictyota dichotoma* from Southern Spain, when samples were exposed to solar radiation depleted from the UVB range and subsequently transferred to dim light conditions. Recovery in samples receiving

either the whole solar spectrum or PAR only, recovered at the same rate. This indicates the presence of complex synergistic effects involved in the inhibition of photosynthesis in the field, which need to be studied further. On the other hand, it must be emphasized that brown algae include many large, perennial species, which exhibit complex responses to UV-exposure. For example, in the southern kelp *Lessonia nigrescens*, the photosynthetic responses to seasonally changing UV conditions form part of the suite of adaptations along with its ontogenic development, i.e., the alga has a complex UVB exposure history characterized by high levels of UVB in summer and low levels in winter (Huovinen et al. 2006). Moreover, gradients in UV tolerance have been reported along of the massive thallus (Gómez et al. 2005b). Thus, the morpho-functional factors involved in UV photobiology of brown algae are important and have to be considered in further studies in order to evaluate more accurately the effects of enhanced UVB on coastal primary productivity.

A common response observed in the brown algal species during acclimation to UV radiation is the reduction in the degree of photoinhibition. This effect may be explained either by the activation of the antioxidative response, increased activity of repair and recovery mechanisms counteracting the inhibitory effects (see above), or by the formation of UV-screening compounds (Lesser 1996).

Mycosporine-like amino acids (MAA)

One of the most important physiochemical acclimation mechanism against biologically harmful UV radiation involves the biosynthesis and accumulation of UV-screening substances. Typically absorbing in the UVA and UVB range, these biomolecules were invoked to function as passive shielding solutes by dissipating the absorbed short wavelength radiation energy in form of harmless heat without generating photochemical reactions (Bandaranayake 1998). The most common photoprotective sunscreens in Antarctic macroalgae are the mycosporine-like amino acids (MAAs), a suite of chemically closely related, colourless, water-soluble, polar and at cellular pH uncharged or zwitterionic amino acid derivatives. MAAs exhibit a high molar absorptivity for UVA and UVB, and have been reported as photochemically stable molecules, which are prerequisites for their sunscreen function (Conde et al. 2000). While MAAs have been mainly observed in numerous Antarctic (Karentz et al. 1991a; Hoyer et al. 2001) and cold-temperate Rhodophyta (Huovinen et al. 2004), Phaeophyta and most Chlorophyta typically lack these compounds, except the green alga *Prasiola crispa* ssp. *antarctica* which contains high concentrations of an unique MAA with an absorption maximum at 324 nm (Hoyer et al. 2001; Karsten et al. 2005). Many Phaeophyta synthesise photoprotective phlorotannins under UV exposure (Pavia et al. 1997; Schoenwaelder 2002b; Schoenwaelder et al. 2003), this strategy will be reviewed in detail below.

The function of MAAs as intracellular screening agents has been inferred from a decrease in concentration with increasing depth (Hoyer et al. 2001, 2003). Supra- and eulittoral Antarctic red algal species experience the strongest insolation, and consequently synthesise and accumulate very high MAA contents, which generally are positively correlated with the natural UV doses (Karsten et al. 1998a; Huovinen et al. 2004). In contrast, many taxa growing in the sublittoral are physiologically not capable to produce MAAs, which well explains their strong sensitivity, for example, of photosynthesis against ambient solar radiation. These Rhodophyta avoid any UV exposure, and, hence, there is no physiological need to synthesise and accumulate metabolically expensive nitrogen-containing MAAs. This in turn would save energy to better support other essential pathways such as light-harvesting phycobilisomes to guarantee sufficient PAR absorption under the prevailing low-light conditions.

While juvenile lateral fronds of the red alga *Palmaria decipiens* collected in Antarctic winter contained low concentrations of UV-absorbing compounds, mature plants in late spring and summer exhibited significantly higher values indicating strong seasonal effects (Post and Larkum 1993), which may be related to the changing daylengths and radiation conditions. Based on the MAA concentrations and the

induction patterns after exposure to different radiation conditions Antarctic Rhodophyta can be physiologically classified in 3 categories (Hoyer et al. 2001): Type I—no MAAs at all; Type II—MAAs inducible in variable concentrations, and Type III—permanently high MAA values. While Type I represents deep-water red algae, Type II and III species are growing in the supra- and eulittoral zone. Experiments with Antarctic Rhodophyta under defined radiation sources indicate that the induction, biosynthesis and accumulation of MAAs is a very flexible and species-specific process. While some taxa synthesise MAAs particularly under UVB, others prefer UVA or higher PAR only (Hoyer et al. 2003). Although experimental evidence for a particular trigger mechanism as well as details for the biosynthetic pathway for individual MAAs are still missing, it is reasonable to assume that a signal transduction pathway must be involved in the overall process leading to high MAA concentrations. Due to the different types of MAA induction patterns the presence of various photoreceptors, most probably between the blue light and UVB wavelengths, have to be taken into consideration (Kräbs et al. 2002).

Not the whole red algal thallus is uniformly responding to the ambient solar conditions, but especially young apical or marginal zones, i.e., growing cells synthesise and accumulate MAAs leading to cross sectional and longitudinal concentration gradients (Hoyer et al. 2001). Older tissue regions exhibit thicker cell walls and a leathery texture, and are therefore optically well protected. In contrast, higher MAA concentrations in the most exposed outer cortex are essential to guarantee protection of the delicate meristematic cells.

Besides the stimulating effect of increasing solar radiation on the biosynthesis and accumulation of MAAs in macroalgae other environmental factors may also act as controlling parameter. Particularly lower temperatures have been experimentally proven to stimulate the MAA concentration of Antarctic Rhodophyta (Hoyer, unpublished data). Nutrient availability may also affect the MAA contents (Korbee et al. 2005). Some MAAs also exhibit antioxidative activity (Dunlap and Yamamoto 1995). However, further functional abilities of MAAs are unexplored in macroalgae.

Also in this example, the genetically determined ability to synthesise UV-screening MAAs in the different species of seaweeds is closely related to the spatial structure of the algal community in the field. In summary, the comparison of the species-dependent ability to form UV-screening compounds under laboratory and field conditions provide strong indications for differential genetic preadaptations to the potentially harmful radiation at the natural growth site.

Phenolic compounds

A special class of polyphenolic compounds are phlorotannins, which are exclusively found in brown seaweeds (Ragan and Glombitza 1986). Phlorotannins are secondary metabolites and occur in tissue concentration of up to 20% of the algal dry weight. Several functions are commonly accepted, including a role in adhesion and a strengthening role in cell walls (Schoenwaelder 2002b). Phlorotannins absorb UV radiation, mainly UVC and partly UVB, with maxima at 195 nm and 265 nm (Ragan and Glombitza 1986; Pavia et al. 1997; Henry and Van Alstyne 2004). As tannins of higher plants, phlorotannins possess a high antioxidant activity. Thus, phlorotannins are important for scavenging cell toxic reactive oxygen species (ROS), such as superoxide anion radicals produced by harmful UVB radiation. Therefore, phlorotannins are proposed to function in protecting against excess irradiance, in particular ultraviolet radiation, by screening UV radiation and/or by being an antioxidant.

We suggest four strategies to consider phlorotannins as UV-protecting compounds (1) a generally high tissue concentration of phlorotannins that absorb harmful radiation and prevent cell damages, (2) an induction of phlorotannins stimulated by harmful radiation, (3) an exudation of phlorotannins in the surrounding medium shielding harmful radiation, or (4) an excess inclusion of phlorotannins in cell walls shielding harmful radiation.

High concentrations of phlorotannins in the outer cell layers protect *Hormosira banksii* from sunburn during Australian summer

(Schoenwaelder 2002a). While the outer cell layers are damaged and disrupted by sunlight, phlorotannins are released from the phlorotannin containing vesicles, the physodes, into the cytoplasma where they cause oxidative burn. Oxidised phlorotannins become brownish and form a dark brownish protective cell layer for the underlying photosynthetic tissue. Similarly, the high density of physodes at the periphery of egg and zygote cells of *Fucus spiralis* is most probably responsible for the high tolerance to UV-exposure, in contrast to *F. serratus*, in which physodes are less abundant (Schoenwaelder and Wiencke 2000; Schoenwaelder et al. 2003).

An induction of phlorotannins after a 2-week exposure of artificial UVB radiation was first described in *Ascophyllum nodosum* (Pavia et al. 1997). A weaker response was found in *A. nodosum* when exposed to natural UVB radiation (Pavia and Brock 2000). In that study significant differences in the phlorotannin content of UVB treated and untreated individuals were found after 7 weeks of exposure to natural UVB radiation, while only slightly increased phlorotannin concentrations were measured in the UVB treated individuals at week 2 and week 4. An induction of phlorotannins due to UVB and UVA radiation was also described for *Macrocystis integrifolia* (Swanson and Druehl 2002). In contrast, no induction of phlorotannins was found in juveniles and embryos of *Fucus gardneri* after 3-week exposure to UV radiation, while growth of embryos was inhibited and growth of juveniles was not affected by UVB radiation (Henry and Van Alstyne 2004). An increase in the size of physodes was observed in various Laminariales from Spitsbergen after UVB exposure indicating an induction of phlorotannin synthesis (Wiencke et al. 2004a). This has recently been verified in the UV tolerant species *Alaria esculenta* and *Saccorhiza dermatodea*. The absorbance of zoospore suspensions from these species increased considerably after UVB exposure, whereas the absorbance of spore suspensions of the UVB sensitive species *L. digitata* did not change at all (Roleda et al. 2006c).

An exudation of phlorotannins as response to artificial UVB radiation was observed in *Macrocystis integrifolia* (Swanson and Druehl 2002). As a result UVB transmission through the water column was reduced, thereby protecting germinating meiospores of *Laminaria groenlandica* against harmful UVB radiation. Similarly, biofilters containing phloroglucinol (the monomer of phlorotannins) mitigated the harmful effect of UV-exposure on developing zygotes and embryos of *Fucus serratus* (Schoenwaelder et al. 2003). Biofilters made of UV transparent acrylic sheet, filled with zoospore suspensions of *S. dermatodea*, *A. esculenta*, *L. digitata* or phloroglucinol showed a varying capacity to protect zoospore cultures from the lethal effects of UVB (Roleda et al. 2006c). Generally, high phlorotannin content and high exudation rates might reflect an adaptation of seaweeds to enhanced UV radiation. Induction and variable exudation rates of phlorotannins reflect the acclimation potential to environmental changes.

Do phlorotannins play a role in the determination of depth zonation of brown algae? Evidence was found in zygotes and embryos of *Fucus* species (Schoenwaelder and Wiencke 2000; Schoenwaelder et al. 2003). *F. spiralis* from the high intertidal zone is less sensitive to UV-exposure and contains much more physodes than *F. serratus*, which is found further down the shore. Similarly, zoospores of *Laminaria digitata*, growing on Helgoland in the upper sublittoral, exhibit a strong absorbance below 300 nm, indicative of phlorotannins, compared to zoospores of the mid and lower sublittoral *Laminaria* species (Roleda et al. 2005a). Phlorotannins may also play a role for the UV-sensitivity of zoospores of Arctic Laminariales from different depths (Wiencke et al. 2004a). Similarly, higher phlorotannin concentrations were found in *Desmarestia anceps* collected in shallow waters compared to deep water samples, which might indicate an induction of phlorotannins due to higher irradiances and/or UV exposure (Fairhead et al. 2005). Conversely, *D. menziesii* shows no differences in phlorotannin concentrations in samples from different collecting depth and even exhibits lower concentrations than *D. anceps*, which usually occurs in deeper waters (Fairhead et al. 2005).

In contrast to the data sets available on potential UV-screens in red and brown algal species information on specific UV-absorbing

compounds in marine green algae is still very limited. Very recent studies demonstrated the solely UVB-induced increase in thallus absorption in *Ulva pertusa* with a maximum at 295 nm (Han and Han 2005), however, the responsible screening compound is still unidentified.

DNA damage and repair

As outlined above, a particularly hazardous event of UV-exposure is the induction of DNA damage. Thus strategies in order to prevent damage or to efficiently repair existing damage represent acclimation mechanisms of crucial importance. Differential induction and accumulation of UVB-induced cyclobutane-pyrimidine dimers (CPD) were measured in several red macroalgae from Brittany and Spitsbergen (van de Poll et al. 2001, 2002). In the course of 15 days repeated exposure to artificial UV radiation, no accumulation of DNA damage but rather a decrease in CPD concentration was observed in the temperate littoral species *Palmaria palmata* and *Chondrus crispus*. Conversely, an approximately 6-fold increase in the amount of CPD was observed in sublittoral species *Phycodrys rubens* and *Polyneura hilliae* (van de Poll et al. 2001). In Arctic red macrophytes, the amount of solar radiation-induced CPD concentrations in *Devaleraea ramentacea*, *Palmaria palmata*, *Odonthalia dentata*, *Coccotylus truncatus* and *Phycodrys rubens* (van de Poll et al. 2002) is related to their upper depth distribution limit in Kongsfjorden described by Wiencke et al. (2004b). In shallow coastal waters, blooms of floating *Ulva* are exposed to the full solar radiation. The amount of thallus DNA damage is, however, relatively low ranging from 1.0 to 1.88 CPD Mb^{-6} depending on solar exposure of the investigated canopy layer (Bischof et al. 2002b) compared to those reported in red macrophytes (van de Poll et al. 2001, 2002). These data suggest that the low sublittoral habitat of the Ceramiales (*P. hilliae*, *C. truncatus* and *P. rubens*) is primarily due to their lack of tolerance to UV radiation and that UV protection mechanisms are not sufficient to prevent the accumulation of DNA-damage in these species.

Obviously, UV-susceptibility of DNA damage is highly depending on the respective developmental stage of the species under investigation. The impact of UVB-induced DNA damage on the early life stages of macroalgae is important in shaping up community structure and zonation pattern. DNA damage in carpospores of eulittoral *Mastocarpus stellatus* and *Chondrus crispus* (Roleda et al. 2004) was lower compared to zoospores of the sublittoral Laminariales in Helgoland (*Laminaria digitata*, *L. saccharina* and *L. hyperborea*; Roleda et al. 2005a) and Spitsbergen (*Saccorhiza dermatodea*, *Alaria esculenta* and *L. digitata*; Roleda et al. unpublished data). The UV-sensitivity of the carpospores and zoospores were related to the depth distribution of the foliose gametophyte and adult sporophytes, respectively. In the subsequent life history stage investigated, young gametophytes and sporophytes were less susceptible to UVB-induced DNA damage compared to spores. No detectable CPDs were observed in the young foliose gametophyte stages of the eulittoral *M. stellatus* and *C. crispus* (Roleda et al. 2004). Conversely, the remaining tissue DNA damage among juvenile Laminariales sporophytes was observed to be dependent on the thallus thickness and optical property (Roleda et al. 2005b, 2006a, 2006b). Increasing thallus thickness and opacity (in relation to available cell-bound UV-absorbing compounds) minimise UV-effects where outer phlorotannin-rich cortical layers can selectively filter short UV-wavelength from reaching the UV-sensitive targets (i.e., chloroplasts).

Less genetic damage was incurred in diploid carpospores compared to haploid zoospores (Roleda 2006). Zoospores were, however, found to be more efficient in DNA damage repair. In a sexual organism, the advantage of both ploidy states can be combined by spending much of the life cycle in the haploid state, then fusing to become diploid. During the diploid state DNA damage can be repaired, since there are two copies of the gene in the cell and one copy is presumed to be undamaged (Long and Michod 1995). In the life history of Laminariales, haploid zoospores were more sensitive to DNA damage compared to the diploid young sporophytes.

Between the investigated Gigartinales, the lower DNA damage and effective DNA damage repair mechanism in carpospores of *M. stellatus* is responsible to its recruitment success and colonization of the upper eulittoral zone effectively changing the rocky intertidal biotope of Helgoland (Roleda et al. 2004).

Acclimation via morphogenetic variation

Several morphogenetic effects have been described for higher plants grown under UVB irradiation. Compared to white light, UVB exposed plants exhibit reduced leaf area and stem growth, but increased leaf thickness (Tevini and Teramura 1989; Mepsted et al. 1996). Information on UV-induced morphogenetic effects on the thalli of marine macroalgae is very limited. Studies on the brown alga *Alaria esculenta* have shown that UVB radiation results in reduced growth in length and a significant increase in fresh weight, indicative for increasing thallus thickness (Michler et al. 2002). In previous studies on various Laminariales and seagrasses it was shown that thicker thalli generally exhibit a higher UV-tolerance than thin thalli (Dawson and Dennison 1996; Dring et al. 1996a; Hanelt et al. 1997b). On the other hand, blades of the southern kelp *Lessonia nigrescens* are more UV sensitive than stipes and holdfasts, which has been though as a strategy to minimise mortality. In this species, the higher UV damage is concentrated in the phylloids, which are transient and with high turnover rate, whereas the massive stipes and holdfast, which are supporting structures, are less exposed to UV radiation (Gómez et al. 2005b). In general, the individual effects of UVB radiation on algal thalli with differences in morphological features are largely unexplored, thus we lack information on how UVB might influence the individual thallus structure of the individual seaweed.

Vertical versus latitudinal distribution

Depth zonation

Ecophysiological studies indicate a general correlation between stress tolerance and vertical distribution of seaweeds (Davison and Pearson 1996; Hanelt 1998). Hitherto, there is agreement that the species sensitivity to solar radiation stress is a function of depth distribution (Dring et al. 1996b; Larkum and Wood 1993; Hanelt et al. 1997a, c; Hanelt 1998; Bischof et al. 1998a; Yakovleva et al. 1998). Moreover, some authors regard solar UVB as one of the most important factors controlling the upper distribution limit of seaweeds in the field (Maegawa et al. 1993). Therefore, it is reasonable to assume that increased UVB, penetrating deeper into the water column, may result in a shift of the upper distribution limit of single species to greater water depths.

Larkum and Wood (1993) were the first who have stressed the correlation between UV-tolerance and the depth-zonation of marine macroalgae. For the vertical distribution of tropical seagrasses UV radiation was also proven to be an important factor (Dawson and Dennison 1996). Dring et al. (1996b) showed that sensitivity to UV in red algae growing around the island of Helgoland (Germany) varies with species and depth of collection. As for UVB radiation, investigations on the photoinhibition induced by high levels of PAR also shows a correlation between depth-zonation and the ability for dynamic photoinhibition of macroalgae both from sublittoral (Hanelt 1992, 1998; Hanelt et al. 1994, 1997a) and intertidal populations (Gómez et al. 2004)

In support of this concept the green algae *Enteromorpha bulbosa* and *Acrosiphonia arcta* which occur in the middle and lower eulittoral at the Antarctic Peninsula (Wiencke and Clayton 2002) do almost show no negative UV-effects on photosynthesis and are able to acclimate to even further elevated UV-exposure within hours or days (Bischof et al. 1998a). In contrast, the brown algae *Desmarestia antarctica* and *D. anceps* are described for the middle sublittoral zone off the Antarctic Peninsula (Klöser et al. 1996) but grow mostly in greater depths and occur only occasionally in depths shallower than 17 m. In these depths biologically relevant doses of UVB radiation occur only in very transparent waters, under clear skies and at a high solar declination (Karentz 1989). This might explain why *D. anceps* is quite sensitive to UVB radiation. The red alga

Gymnogongrus antarcticus occurs from the upper sublittoral zone down to 20 m (Klöser et al. 1996), i.e., the upper distribution limit is similar to that of the brown algae *D. anceps* and *Himantothallus grandifolius* and upon UVB exposure these three species show a similar inhibition rate of photosynthesis. *H. grandifolius* is found at 5 m (Lamb and Zimmermann 1977) with the lowest depth at 90 m (Zielinski 1990). This zonation pattern is in line with its high sensitivity. Finally, the red algae *Phycodrys austrogeorgica* and *Delesseria lancifolia* are described for the middle sublittoral zone (Delaca and Lipps 1976; Zielinski 1990; Klöser et al. 1996), but they grow under canopy plants such as *D. anceps* and *H. grandifolius*. This explains their extreme sensitivity to UV radiation. These plants may lack all protecting mechanisms against excessive radiation, because recovery from UV-exposure is poor in both species. The observed differences in species dependent UV-sensitivity are as outlined above genetically determined.

The decisive role of UVB radiation in determining vertical zonation patterns in seaweeds was recently evidenced in studies on the UV effects on the particularly sensitive developmental and reproductive stages. Only few studies were conducted using the unicellular propagation units of seaweeds, although it is widely recognised that the early developmental stages are the most susceptible to a variety of anthropogenic stresses (Coelho et al. 2000).

Seaweed propagules, spores, gametes and zygotes, are the unicellular products of asexual and sexual reproduction and have essential functions in the life-history of seaweeds with respect to dispersal, settlement, attachment, survival and recruitment (Clayton 1992; Norton 1992). They are naked cells, bounded by a plasma membrane, and in some species covered by a layer of mucilage. Their size ranges from 2 μm to >250 μm in diameter and determines the sinking rate in the water column (Okuda and Neushul 1981). Brown and green algal spores and gametes are flagellated and usually small, between 3 μm and 10 μm in diameter (Henry and Cole 1982; Clayton 1992). Zygotes of the brown algal order Fucales have diameters between 60 μm and 250 μm (Clayton 1992; Schoenwaelder et al. 2003). Spores of red algae are between about 10–100 μm in diameter (Clayton 1992). A positive phototaxis is found in spores of the brown algal genus *Ectocarpus* (Müller 1977) and the green algal genus *Ulva* (Evans and Cristie 1970), a negative phototaxis is found in some primitive Laminariales including *Saccorhiza dermatodea*. However, the capability for active swimming over long distances is rather limited. Even motile propagules have little control over their fate. The range of dispersal is at least 200 m and is driven mainly by currents and water motion (Norton 1992; Frederiksen et al. 1995). The number of chloroplasts per propagule can be very low. The zoospores e.g. of the more advanced families of the Laminariales, the Alariaceae, Laminariaceae and Lessoniaceae only contain one small chloroplast (Henry and Cole 1982), with comparatively low photosynthetic activity (Amsler and Neushul 1991; Wiencke et al. 2000). Storage lipids are certainly the main energy source of spores, supporting swimming and potentially germination processes (Brezezinski et al. 1993; Reed et al. 1999).

Among the different stages in the life-cycle of seaweeds the unicellular propagules are clearly the stages most susceptible to UV radiation. Germination of *Ectocarpus rhodochondroides* spores is inhibited by UVB, while adult specimens survive (Santas et al. 1998). Similarly, the photosynthetic efficiencies (F_v/F_m) of sporophytes and zoospores of *Laminaria digitata* differ strongly when exposed to PAR, PAR + UVA or PAR + UVA + UVB (Wiencke et al. 2000). Irrespective of the radiation treatment large sporophytes show always considerably higher F_v/F_m values compared to zoospores. Motile zoospores of *Lessonia nigrescens* and *L. trabeculata* from Chile are more UV susceptible than settled spores, gametophytes and young sporophytes (Véliz et al. 2006). The macrothalli of red algae *Mastocarpus stellatus* and *Chondrus crispus* are relatively UV tolerant whereas their carpospores are not (Bischof et al. 2000b; Roleda et al. 2004). Similarly, photosynthetic efficiency of zoospores of the green alga *Ulva intestinalis* exhibits an up to 6-fold higher UVB sensitivity compared to the mature thalli (Cordi et al. 2001). Interestingly, the UV susceptibility of the gametes is even greater.

The UV susceptibility of the photosynthesis and of the DNA in spores is unequivocally related to the depth distribution of the macrothalli as outlined above (see chapters 5.1, 5.1.1.3; Bischof et al. 2000a; Wiencke et al. 2000; Roleda et al. 2004, 2005a). Other negative effects of UV radiation especially on macroalgal spores presumably important for determination of the upper distribution limit concern the cytoskeleton. The phototactic response of zoids of the brown algae *Scytosiphon lomentaria* and *Petalonia fascia* is negatively influenced by UVB (Flores-Moya et al. 2002). Moreover, the motility of zoospores of *L. saccharina* is affected by UVB depending on the actual UV doses (Makarov and Voskoboinikov 2001). This might be related to the observation by Huovinen et al. (2000) who reported that the nuclear division of spores of *Macrocystis pyrifera* is inhibited after UVB exposure. Both nuclear division and the activity of the flagellar apparatus depend on a functional microtubular system, which might be damaged by UV. This would explain also the drastic affects on zygotes observed in *Fucus serratus* and *F. distichus* (Schoenwaelder et al. 2003). No polarisation has been observed in UV exposed zygotes, rather, they remain spherical and there is no further development. Similarly, amphibian and fish zygotes remain undifferentiated and this has been related to UV effects on the microtubuli (Scharf and Gerhard 1983; Strahle and Jesuthasan 1993). The actin cytoskeleton may be affected as well as studies on other fucoids suggest. Actin inhibitors prevent polarisation, cross wall formation and vesicle movement (Schoenwaelder and Clayton 1999), the same effect as after UV treatment of zygotes of the two *Fucus* species (Schoenwaelder et al. 2003).

In spores the balance between the damaging effects of UV radiation and the various repair and protective mechanisms is indicated by the integrative parameter germination. If germination is not inhibited after UV exposure the repair and protective mechanisms are strong enough to outweigh the damaging effects of UV. Spore vitality after UV exposure in *M. stellatus* is higher compared to *C. crispus*, probably due to the higher capability for DNA repair in *Mastocarpus* (Roleda et al. 2004). In this context the size of the algal propagules may be of importance as the UV susceptibility of zoospores of various Laminariales from the eastern Pacific depends on the size of the spores (Swanson and Druehl 2000). The spores most tolerant to UV stress come from shallow water species, whereas the progeny of kelps occupying low-level UV-environments exhibit a lower germination capacity after UV stress. These results are similar to studies of phytoplankton species, in which larger organisms are more tolerant to UV exposure (Karentz et al. 1991b).

A clear dependence of the UV susceptibility of germination and growth of sporelings of coralline algae on the radiation conditions in the habitat of the various species has been demonstrated by Bañares et al. (2002). Spores from species in sun-exposed habitats in the eulittoral were more UV tolerant than spores from a species growing in shaded crevices. Similarly, zygotes of *F. serratus* from the mid eulittoral on Helgoland show an abnormal development after UV exposure, whereas zygotes of *F. spiralis*, a species from the upper eulittoral much stronger exposed to UV, is not affected by the same UV treatment (Schoenwaelder et al. 2003). A clear dependence of the upper depth distribution limit of seaweeds on the UV susceptibility of their spores has also been proven for the three *Laminaria* species from Helgoland mainly due to the different DNA repair capacities and the different content of UV absorbing compounds (Roleda et al. 2005a). Similarly, the UV tolerance of different brown algae from Spitsbergen determines the upper depth distribution limit as indicated by experiments in the laboratory (Wiencke et al. 2000, 2004) and in the field (Wiencke et al. 2006).

Microscale gradients in UVB exposure

Pronounced acclimation of photosynthesis to UV exposure does also take place along microscale gradients as for example in algal mats: Green algal mats do frequently occur as a result of eutrophication in sheltered coastal lagoons. Within these mats usually a steep gradient of solar radiation occurs (Vergara et al. 1997): Top layers are exposed to high surface irradiance, whereas bottom layers are permanently exposed

to very low light conditions or even stay in darkness. It has been show for the two bloom-forming green algal species *Ulva rotundata* and *Chaetomorpha linum* that UVB irradiance substantially contributes in structuring these mat-like canopies (Bischof et al. 2002b, 2003, 2006). Inside the mats, strong gradients are visible for solar (UVB) radiation, but also for physiological responses: loss in photosynthetic pigments and proteins is strongly pronounced in top layers and is diminished with increasing depth inside the mat. Photosynthetic activity is inhibited in the top layers, performs at maximum rates in intermediate thallus layers and, due to light limitation, is again strongly reduced in bottom layers (Krause-Jensen et al. 1996; Vergara et al. 1997; Bischof et al. 2002b). A specific response to the degree of UVB exposure inside these mat-like structures is the specific activity of superoxide dismutase (SOD), an enzyme responsible for the scavenging of superoxide anions generated in photosynthesis under stress full conditions (Bischof et al. 2003, 2006). Depending on the degree of UVB exposure and inhibition of photosynthesis along the depth gradient, the activity of SOD becomes stimulated. Two mechanisms might be involved in this response: either the enzyme becomes activated due to a light effect (due to exposure to short wavelength radiation) or it is the presence of previously generated oxygen radicals (ROS) which act as trigger for increasing SOD activity (Bischof et al. 2006). For higher plants, it was shown that ROS play an important signalling role in signal transduction pathways, in order to respond to UVB exposure (Mackerness et al. 1999).

From the tropics to the poles

As the problem of ozone depletion is rather restricted to the polar and temperate regions, organisms inhabiting the (shallow water zone of) tropical regions are unlikely to be affected by seasonally *enhanced* UVB irradiance, but are of course permanently exposed to much higher UV levels than encountered in polar regions (even under ozone depleted conditions). Thus, tropical species must have developed particularly effective protection strategies in response to high UVB irradiance. Unfortunately, data on UVB protection in tropical species as well as comparative studies on related species from different geographical regions are extremely scarce and the limited information available is not conclusive. In a study on different species of the green alga genus *Cladophora* no hints were found for a particular higher UVB tolerance of a true tropical species (*C. zolingerii* from the Philippines) compared to its cold-temperate congener *C. rupestris* (Bischof and van de Poll unpublished data). Preliminary data on UVB absorption characteristics within the cell wall of both species did not provide any hint for a more effective UVB shielding in the tropical species. Moreover, also physiological parameters tested did not point to a particularly higher UVB tolerance of the tropical species compared to the congener from temperate waters.

Like at the species level, studies on latitudinal UV-patterns at the community level are extremely scarce. To our knowledge, only the study by Wahl et al. (2004) investigated UV-effects on shallow-water macro-epibenthic assemblages at different bio-geographical regions. Their study revealed a consistent pattern of UV-effects at both hemispheres. Species richness and community biomass were negatively affected by UV-treatments. Surprisingly, effects by UVA were more detrimental than those of UVB. UV-effects were transient, disappearing at 80% of all sites within 2–3 months, but persisted at one polar (Norway) and one tropical (China) site, suggesting lack of latitudinal patterns of UV-effects at the community level.

Ecological implications—UVB and the structure of seaweed communities

The consequences of enhanced UVB exposure to ecosystem function are still largely unexplored and hypothetical. However, based on the studies accomplished so far the following assumptions can be made.

Potential effects on primary productivity

Throughout the previous studies, it is shown that all species, which have to withstand UVB in the

field (i.e., the species inhabiting the intertidal and the upper sublittoral zone) possess different and largely efficient mechanisms for acclimation to respond to changes in light climate. However, formation of screening compounds as well as the development of further protective mechanisms require additional energy costs, which may result in reduced growth and primary productivity (Roleda et al. 2006a). This problem is still largely unaddressed but an important field of future investigation. As long as the energy costs for applying protective mechanisms remain unknown a reduction of seaweed productivity in response to increased UVB levels in future cannot be excluded.

Reduced reproductive success and shifts in age structure

The information available on UV-susceptibility of different developmental stages indicates the unicellular spores and zygotes as being most sensitive. Other information on how UV-exposure may affect reproduction and the timing of developmental cycles is hardly available. It is obvious that increased UV-induced spore mortality will result in impaired reproductive success, but may also affect the age structure of seaweed populations (Wiencke et al. 2000, 2004a). Due to high interannual variations in light climate particularly in polar areas (Hanelt et al. 2001) high UV-irradiance may affect zoospore survival in shallow waters in 1 year, as in another year it may not. Thus new recruits are only likely to develop to adult sporophytes if they are protected from high UVB exposure. In certain years with particularly high fluences of UVB reaching the benthic communities a new generation of recruits might therefore fail to develop, while larger age and size classes of sporophytes were rather unaffected due to the already accomplished acclimation on a physiological and morphological base (Altamirano et al. 2003a, b).

Downward shifts in depth distribution

As outlined above there is now evidence, that the species sensitivity to solar radiation stress is a function of depth distribution (Larkum and Wood

1993; Dring et al. 1996b; Hanelt et al. 1997a, c; Hanelt 1998; Bischof et al. 1998a; Wiencke et al. 2006). For several physiological parameters a strong correlation of UVB sensitivity and vertical position on the shore was shown for numerous species (van de Poll et al. 2001, 2002; Bischof et al. 1998a, Gómez et al. 2004, Wiencke et al. 2006). Therefore, it is reasonable to argue that increased UVB, penetrating deeper into the water column, results in a shift of the upper distribution limit of single species to greater water depths. However, at least in the macrothalli several acclimation processes can counteract radiation stress, but the particular sensitivity of spores may be the decisive aspect in this scenario, thus preventing recruitment in shallow waters with high UVB irradiances. Through this process, elevated UVB may result in a shift of seaweed communities to deeper waters (Wiencke et al. 2006).

Succession

Species do not exist in isolation. Rather, multiple species form complex, interacting habitat-specific communities. Results from physiological studies at the species level might not reflect biological responses when repeated at the community level due to e.g., indirect or synergistic effects. Consequently, it seems reasonable that an ultimate assessment of UV-effects should be inferred at the community level (Bothwell et al. 1994). Open space represents a key resource for many species of seaweeds and its colonisation is characterised by a series of species replacements (Sousa and Connell 1992). Three alternative successional models have been proposed by Connell and Slatyer (1977). The facilitation model suggests that initially the propagules of a few species will recruit on open space and their existence will modify the substratum for the settlement of other species. The tolerance model predicts a neutral effect of early on later colonizers with the latter replacing early colonizers due to more efficient resource use by competitive exclusion. Under the inhibition model, early settlers pre-empt the substratum, hindering invasion of subsequent species. The predictions of these models may be altered by overlaying patterns of climatic or

ecological factors (e.g., grazing Farrell 1991; Sousa and Connell 1992).

Only a few studies assessed UV-effects during species succession of shallow-water seaweed-dominated communities (Santas et al. 1998; Lotze et al. 2002; Molis et al. 2003; Molis and Wahl 2004; Wahl et al. 2004; Dobretsov et al. 2005). Surprisingly in all but one study (Dobretsov et al. 2005), UV-effects were only apparent during the early phase of succession. In the study by Dobretsov et al. (2005) it seemed very unlikely that later successional species could cope with UV-effects by acclimatizing at the same time to the UV-regime, e.g., by induction of UV-screening substances. Alternatively and more likely, transient UV-effects during community assemblage might result from intra- and interspecific differences in the susceptibility to UV-exposure for which experimental evidence exists. For instance, differential UV-sensitivities of carpospores influenced recruitment success of two competing Gigartinales-species, partly explaining vertical zonation patterns of both species (Roleda et al. 2004). Similarly, spores from deeper dwelling species exhibit higher mortality rates compared to spores from shallow water species (Wiencke et al. 2000, 2004a, 2006). Moreover, sorus of *Laminaria digitata* is completely opaque, resulting in a sudden and drastic change in UV-exposure ('UV-shock') for released zoospores (Gruber, pers. communication). Finally, several seaweed species, e.g. green filamentous forms, seem particularly well adapted to recruit at UV-exposed sites in the upper eulittoral, i.e., where UV-irradiance is strongest on the shore, and it was experimentally demonstrated that their abundance correlates positively with UV-exposure time (Molis et al. 2003). The invasion of sites high on the intertidal shore might be a selective advantage, as this guarantees a relative shorter exposure to grazers compared to sites lower on the shore. Thus, macroalgal propagules may show species-specific differential UV-sensitivities, which favour initial colonisation of empty space by UV-resistant species. Wahl et al. (2004) suggested that these early colonizers facilitate the recruitment of later successional seaweed and invertebrate species at the majority of their study sites by amelioration of UV-regimes due to

protective shading. Similarly Vinebrooke and Leavitt (1999) concluded that diatom mats can precondition the substratum for macroalgal spores by provision of UV-free micro-climates.

The effect of UVB exposure on the early succession of macroalgae was also studied at a rocky intertidal platform at King George Island, Antarctica, revealing a significant reduction of species diversity based on the effects of UVB (Zacher et al. unpublished data). Species recruitment and dry weight was monitored over a period of 15 weeks on artificial substrates exposed in the intertidal zone. Natural UV-exposure was found to affect the density of the green alga *Monostroma hariotii* in the first 10 weeks of the experiment, whereas the density of red algal recruits decreased significantly due to UV after 8 and 15 weeks, respectively. Shannon diversity *H'* dropped as succession proceeded in the PAR + UVA + UVB treatment, increased slightly in the PAR + UVA treatment, and increased in the PAR treatment from the beginning until the end of the experiment. Furthermore, the treatment with PAR alone resulted in a significantly higher diversity at the end of the experiment than the treatment including the total UV-range. After 15 weeks the community excluded from UV radiation showed a significantly higher diversity, evenness and number of red algal germlings and species than communities exposed to the whole solar spectrum. This led to a significant dissimilarity in species composition between these two communities. Diversity was negatively influenced by both UVA and UVB radiation. The results show that Antarctic macroalgal recruits are particularly sensitive to UV-exposure during their first month of development, but that effects change during succession.

Competition

Very few examples of UV-mediated changes in competitive abilities of macroalgae exist (Bischof et al. 2000b; Roleda et al. 2004). However, UV-exposure may quite commonly affect the competitive ability of a macroalgae, if UV-induced changes, e.g., production of MAAs, represent a metabolic cost for the alga. Moreover, the competitive ability of seaweeds may be negatively

affected, if UVB has detrimental effects on growth. As a result, the algae will be shaded by more UV-resistant species and experience further reduced growth due to limited PAR-regimes, similar to what has been predicted for terrestrial plants (Caldwell et al. 1989).

Several species of algae are known to affect the community structure of nearby developing benthic assemblages (Wahl 2001). One possible mechanism of this biogenic neighbourhood effect is the exudation of metabolites that influence settlement. Little is known about UV-induced changes in chemical composition of macroalgal exudates and the possible indirect effects of UV-exposure on the structure and species composition of communities that establish in the vicinity of macroalgae. For example, tri-hydroxycoumarins (phenolics) excreted by the green alga *Dasycladus vermicularis* in response to enhanced radiation conditions protects other macroalgal species from UV-exposure (Pérez-Rodriguez 2000). UV-resistant seaweeds may have a selective advantage over UV-sensitive species by indirectly reducing herbivory. Given that two species of macroalgae have identical physiological properties, except with respect to UV-susceptibility, one would expect the less sensitive species to occur higher on the shore, i.e., where UV-regimes are more severe than lower on the shore, than the UV-sensitive counterpart. Consequently, the UV-sensitive species would be exposed over longer periods to motile consumers, e.g., isopods, and other important herbivores, e.g. sea urchins.

Alga-herbivore interactions

The consumption of plant biomass represents the most fundamental plant-animal interaction, affecting biomass accrual and community composition of photoautotrophs (Sousa and Connell 1992; Duffy and Hay 2000). Consequently, herbivory is one key factor controlling the central ecosystem services of primary producers. Grazing intensity is considered to be lower on terrestrial plants than on aquatic macrophytes (Cyr and Pace 1993), due to a higher availability of seaweed biomass to herbivore attacks, the larger proportion of digestible algal biomass (Hay 1991), and

higher mass-specific consumption rates of aquatic herbivores (Cyr and Pace 1993). As a result, aquatic plants may be more strongly top-down controlled than terrestrial counterparts and, thus, trophic interactions in aquatic habitats may be of stronger ecological outreach, e.g., in driving algal recruitment (Diaz-Pulido and McCook 2003), community succession (Farrell 1991) or mediating stability-diversity-productivity relationships of communities (Worm and Duffy 2003).

Seaweeds actively participate in the interaction with herbivores by tolerating consumption with compensatory growth (Cronin 2001), escape from herbivory (Hay et al. 1988), or the defence of grazing (e.g., Cronin 2001). Anti-herbivory defences in seaweeds may either be permanently expressed (constitutive) or induced in response to herbivory (Amsler and Fairhead 2006). Experimental evidence suggests that the induction of anti-herbivory defences is of selective advantage in variable grazing regimes (Karban and Nagasaka 2004), while constitutive defences are more beneficial to algae under a constant herbivory load (Karban et al. 1999). Induced chemical anti-herbivory defences can result in reduced consumption of previously attacked tissues (Ceh et al. 2005), increased feeding dispersal with a concomitant higher risk of herbivores becoming visible to predators (Borell et al. 2004) or both (Borell et al. 2004). The induction of anti-herbivory defences in seaweeds is known to be tissue- and (Sotka et al. 2002; Taylor et al. 2002) grazer-specific (Pavia and Toth 2000; Molis et al. 2006) and that at least some of this specificity is seasonally variable (Molis et al. 2006). Thus, phenotypic plasticity of algal responses to herbivory adds complexity to the trophic interactions between algae and their consumers. Furthermore, seasonality in inducible defences suggests that top-down forces may vary under variable environmental conditions, e.g., UV-regimes.

Cronin and Hay (1996) reported that UV-exposure reduced chemical defences in *Dictyota ciliolata*, making this brown seaweed more palatable to sea urchins and to a lesser extend also to amphipods. The selected UV-exposure time represents common emergence periods for intertidal algae. Consequently, UV-exposure seems to have

the potential to increase algal susceptibility to consumers, especially during summer, i.e., at maximum UV-levels. However, algae form multi-layered piles during low tide, suggesting that only top-layered individuals are fully affected by UV, while specimens positioned deeper in the pile are protected to some extend from UV-exposure. Similar indirect UV-protective effects are known from cyanobacterial mats (Karsten et al. 1998b) and macroalgal dominated subtidal macrobenthic communities (Wahl et al. 2004). Furthermore, UV-effects on algae-animal interactions were absent in the study of Macaya et al. (2005) who did not detect any changes in response patterns between UV-exposed and -shielded *Macrocystis* individuals. This suggests that UV-exposure did not alter the ability to induce anti-herbivory defences in this brown macroalga, at least in the case of some invertebrates. Lotze and Worm (2002) investigated the interactive effects of UV-exposure and grazing on early life stages of a green alga. Their study revealed that the influence of ecological controls, i.e., grazers, on *Enteromorpha*-recruitment were stronger than climatic controls, i.e., UV and temperature, and of opposite sign.

Linking UV-effects on macroalgae with trophic interactions seems to be an interesting, but as yet not fully accounted venue for further exploiting the effects of climatic and ecological drivers on the performance and fitness of seaweeds and the species composition and productivity of seaweed communities. Presently, too few studies tested the interactive effects of UV-exposure and herbivory on alga-consumer interactions to draw general conclusions about the influence of UV-radiation on herbivory. It seems likely that UV-induced chemicals may indirectly change the susceptibility of algae to consumers by altering the function of existing chemicals, which could in- or decrease algal palatability. Alternatively, UV-induced compounds may have multiple functions. Schmitt et al. (1995) demonstrated that herbivore-deterrent chemicals displayed also anti-fouling activities. To our knowledge, only the study by Pavia et al. (1997) suggests multiple functions in UV-induced phlorotannins. The concentration of phlorotannins was lower in controls than in UV-exposed *Ascophyllum nodosum*, with the latter stimulating *Idotea* grazing. As UV-exposure is known to induce the production of many secondary metabolites (e.g., MAAs) it would be interesting to study the direct and indirect effects of these compounds on algae-herbivore interactions. For instance, UV-induced secondary metabolites may affect the anti-fouling ability of a macroalgae and altered epibiontic communities may change algal susceptibility to consumers, resulting in shared doom scenarios or associational resistance (*sensu* Wahl and Hay 1995).

Besides UV-induced effects on macroalgae, patterns of herbivory can also be altered by UV-effects on consumers. McNamara and Hill (1999) showed differential susceptibility of consumers to UVB, suggesting shifts in grazing regimes at sites of high UVB-exposure. Experimental evidence comes from studies on periphyton communities. DeNicola and Hoagland (1996) showed that herbivore density under UV-exposure was on average 50% reduced compared to PAR-treatments at the end of a 28 d long experiment. Bothwell et al. (1994) reported that, in the presence of herbivores, biomass accrual in UVB-exposed periphyton communities was higher than in PAR-irradiated communities. This suggests stronger negative effects at the consumer than at the producer level and, consequently, an indirect positive UVB-effect on periphytic biomass production. Future studies should focus on UV-effects on herbivores to elicit the relative harmfulness of UV-exposure on seaweeds and their consumers.

Synthesis

Under present radiation conditions, UVB radiation has already to be regarded as a common abiotic factor, which influences the physiology of individual seaweeds but does also contribute in structuring seaweed communities in various ways. However, its potential threat to biologic processes is counteracted by several adaptive strategies activating different protective and repair mechanisms. These mechanisms (e.g., formation of screening compounds, antioxidative systems, regulation of enzyme activity and gene expression, DNA repair mechanisms) serve as a physiological filter to reduce the adverse effect of the impinging

solar UVB, in addition canopy algae also protect more susceptible subcanopy organisms from solar exposure. Based on the differential adaptation and acclimation capabilities realised in the different species UVB radiation may, even under non-depleted ozone conditions, substantially affect the structure of seaweed communities. As outlined above, UVB exposure may modulate productivity, reproduction, vertical distribution, species diversity and succession, competition and alga-herbivore interactions. However, the effect extent of each of the aspects under ozone-depleted conditions is largely unknown. To improve our knowledge on how UVB may shape seaweed communities and thus rocky coastal ecosystems in the future, further research should predominantly focus on the following three directions: (1.) UVB is not the only factor potentially causing abiotic stress to seaweed photosynthesis. Particularly the intertidal zone is characterized by large variation of abiotic parameters, furthermore anthropogenically caused increases in seawater temperature and nutrient loads also affect seaweed performance in the field. Physiological studies on the interaction of a multitude of abiotic (stress) factors are indispensable. (2.) The molecular mechanisms triggering acclimation strategies are largely unknown. The application of molecular tools also in seaweed physiology will be a major step forward in this respect. (3.) Certainly, the most serious lack of information is still present regarding the ecological interactions modulated by UVB exposure. As outlined above, only fragmentary data sets are available so far addressing how UVB is presently interfering with seaweed succession or in interactions with seaweed-associated consumers. Field studies on a large spatial and time scale would be required including the generation of UV-free, ambient UV and increased UV irradiation treatments. Such as kind of experiment is logistically ambitious but would substantially broaden our knowledge on how UVB will alter the structure of seaweed communities in the future.

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