Effects of enhanced UV-radiation on photosynthesis of Arctic/cold-temperate macroalgae

Effekte erhöhter UV-Strahlung auf die Photosynthese arktisch/kalt-gemäßigter Makroalgen

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Contents

ABBREVIATIONS

Abs	absorbance
ATP	adenosin-triphosphate
BED	biological effective dose
BWF	biological weighting function
Chl *a*	chlorophyll *a*
CO_2	carbon dioxide
D_1	reaction centre protein 1 of PS II
$\Delta F/Fm'$	effective quantum yield of photosynthesis
Da	dalton
DNA	desoxyribonucleic acid
DOM	dissolved organic matter
DU	Dobson units
ETRmax	maximal relative electron transport rate
Fm	maximal chlorophyll fluorescence of samples previously acclimated to darkness
Fm´	maximal chlorophyll fluorescence of irradiated samples
Fo	minimal fluorescence of dark acclimated samples
Fv	variable chlorophyll fluorescence
Fv/Fm	maximal quantum yield of photosynthesis
G3PDH	glyceraldehyde-3-phosphate dehydrogenase
J	joule
K_d	vertical attenuation coefficient of downward irradiance
λ	wavelength
LHC	light harvesting complex
MAA	mycosporine-like amino acid
$NADH_2$	nicotine adenine dinucleotide (reduced form)
NAD^+	nicotine adenine dinucleotide (oxidised form)
nm	nanometer
O_2	molecular oxygen
O_3	ozone
PAM	pulse amplitude modulated

PAR	photosynthetically active radiation (400-700 nm)
PGK	phosphoglycerate kinase
PI-curve	photosynthesis *versus* irradiance curve
PS I	photosystem I
PS II	photosystem II
PSC	polar stratospheric clouds
qP	photochemical quenching of chlorophyll fluorescence
qN	non-photochemical quenching of chlorophyll fluorescence
RNA	ribonucleic acid
ROS	reactive oxygen species
RubisCO	ribulose-1,5-bisphosphate carboxylase/oxygenase
SDS-PAGE	Sodiumdodecylsulphate polyacrylamide gel-electrophoresis
SOD	superoxide dismutase
UVA	ultraviolet A radiation (320-400 nm)
UVB	ultraviolet B radiation (280-320 nm)
UVC	ultraviolet C radiation (190-280 nm)
UVR	ultraviolet radiation (190-400 nm)
W	watt

SUMMARY

Arctic macroalgae are subjected to strong seasonal and daily changes in the radiation climate. They are exposed to six months of darkness during the polar night, but also suddenly exposed to high radiation in spring after the break-up of the sea ice, especially during low tide at high water transparency. Elevated levels of UVB radiation (UVB), resulting from stratospheric ozone depletion, also contribute to high radiation stress. The investigations presented here were conducted to study the effects of enhanced UV-radiation (UVR) on the physiology of Arctic/cold temperate macroalgae in the laboratory and in the field. The results present a basis for predicting future changes within Arctic coastal ecosystems with respect to increasing UVB levels.

Radiation conditions in the Arctic change dramatically with the seasons. At the study site (Kongsfjord, Spitsbergen) at approx. 80° North, the polar night lasts from mid October until mid February, the polar day from mid April to mid August. Maximal irradiances on the surface are about 1300 µmol photons $m^{-2}s^{-1}$ of photosynthetically active radiation (PAR; 400-700 nm), 19 Wm^{-2} UVA (320-400 nm) and 1,09 Wm^{-2} UVB (280-320 nm). The UVB irradiance is strongly dependent on the actual ozone concentration in the stratosphere, as confirmed spectrometrically by radiation measurements. The light climate in the water column is highly variable. Dissolved organic matter (DOM), sediment, phytoplankton blooms, as well as the tidal cycle determine additionally the *in situ* radiation conditions of macroalgae. The deepest penetration of UVB into the water column of the Kongsfjord has been determined at 10 m depth.

Numerous biological processes, such as photosynthesis, are impaired by UVB. The degree of UVR induced inhibition of photosynthesis as well as the potential to acclimate to changing radiation conditions is species dependent, as demonstrated by field experiments on different algal species which were collected in deeper waters and transplanted to shallow waters. Maximal quantum yield of photosynthesis acclimates rapidly to increased radiation conditions in species characteristic for the upper sublittoral zone (e.g. *Palmaria palmata*), while photosynthesis in species from deeper waters (e.g. *Phycodrys rubens*, *Ptilota plumosa*) is significantly impaired. These experiments indicate that the ability to acclimate to irradiance changes is genetically fixed.

Different processes involved in photosynthesis are impaired by UVR exposure. The adverse effects of UVR on the Calvin cycle enzymes ribulose-1,5-bisphosphate carboxylase/oxygenase (RubisCO) and glyceraldehyde-3-phosphate dehydrogenase (G3PDH) in marine macroalgae were studied for the first time. RubisCO is particularly sensitive to UVR exposure. Reduced photosynthetic electron transport rates may be related to decreasing RubisCO activity, which is, partly a result of the degradation of the protein. In the brown alga *Alaria esculenta*, the formation of a high molecular weight polypetide was observed during UVR exposure, in parallel with decreasing concentration of the large and small subunit of RubisCO, indicating an aggregation of degraded protein. In contrast to RubisCO, G3PDH is more resistant to UVR exposure. The different sensitivity of photosynthetic reactions reflects the zonation patterns of the species examined in the field.

Exposure to UVR can cause detrimental effects on photosynthesis, and macroalgae have developed acclimation strategies to cope with the drastic changes in irradiance. Acclimation of photosynthesis to changing radiation was studied in the brown algae *Laminaria saccharina, Alaria esculenta, Saccorhiza dermatodea*, collected at different water depths. Maximal quantum yield of photosynthesis in specimens collected in greater water depth is significantly more strongly impaired than in shallow water algae of the same species and exposed to the same fluence of artificial UVR. The ability to acclimate to various radiation conditions seems to be necessary for growth over a wide range of water depths.

The time course of acclimation of photosynthesis to enhanced levels of white light and UVR has been studied in the brown alga *Alaria esculenta*. Low light acclimated algae were collected in spring under sea ice and exposed to repeated exposure cycles of different radiation conditions. Maximal quantum yield acclimates significantly within a few days. During the first exposure cycle, photosynthesis is primarily impaired and recovery from inhibition proceeds slowly. However, after some days of treatment, the capacity for recovery is increasing significantly and inhibition is reduced. In samples previously acclimated to high levels of PAR and exposed to high PAR supplemented with UVR, no additional UVR-inhibition of photosynthesis occurs, but recovery proceeds significantly more slowly. This indicates that photoinhibition is predominantly caused by white light, whereas UVR slows down the recovery process.

In situ experiments with the brown alga *Laminaria saccharina* and the red alga *Palmaria palmata* show, that photosynthesis is hardly impaired by UVB irradiation at the natural growth site of these species, as they are protected by the water column above. After irradiance is increased by transplanting the algae from 3 to 1 m water depth, the maximal quantum yield of photosynthesis acclimates stepwise. An additional UVR treatment in the laboratory does not further impair the algae, previously kept at 1 m water depth. In contrast, samples from greater depth are very sensitive to the artificial UVR treatment.

A possible protective mechanism against increasing UVR is the synthesis of UVR screening compounds. In the Arctic endemic red alga *Devaleraea ramentacea*, the synthesis of UVR screening mycosporine-like amino acids (MAAs) has been studied. These substances are commonly found in various red algal species from shallow waters and are shown to provide partial protection of photosynthesis against UVR induced inhibition. In *D. ramentacea* the synthesis of MAAs is predominantly induced by the UVB component of the solar spectrum, as shown by UVR exclusion experiments in the field. The internal MAA concentration is determined by several factors all depending on solar radiation. Specimens from the same collecting site exhibit much higher MAA concentration when sampled in August (at the end of the Arctic summer) as when being sampled in May. The content of MAAs is also related to collection depth, with algae from shallow waters containing significantly higher concentrations of MAAs than deep water samples. There is also a marked gradient of MAA concentration within the thallus. The sun-exposed tips contain higher concentrations of MAAs than the shaded base.

The respective concentration and composition of MAAs is species dependent. The accumulation of high concentrations of MAAs might be linked to the respective vertical distribution of species on the shore. This aspect was studied in the closely related red algal species *Chondrus crispus* and *Mastocarpus stellatus* from the island of Helgoland. Thalli of both species were collected from the same location and exposed to artificial UVR radiation. Photosynthesis in *C. crispus* responds more sensitively to UVR than *M. stellatus*, which might be related to the highly different MAA composition. *M. stellatus* contains up to 6-fold higher concentrations of MAAs than *C. crispus*, probably allowing *M. stellatus* to grow at locations more exposed to the sun.

Different life history stages exhibit strong differences in UVR tolerance. In particular, brown algal zoospores are very sensitive to UVR exposure. Photosynthesis of spores is more strongly impaired by UVR than that of large sporophytes, and results in an increased mortality of spores. Spores of different species from the Arctic and Southern Spain and exposed to the same dose of UVR, show that the viability is species dependent. Spore mortality of species that are commonly growing in the lower sublittoral zone (e.g. *Laminaria saccharina*) is higher than from species growing in shallow waters (e.g. *Chordaria flagelliformis*). The mortality of *Laminaria digitata* spores is positively correlated with the formation of thymine dimers indicative for DNA damage. UVR irradiances in Southern Spain, commonly measured in water depths shallower than 7 m, induce mortality in spores of four species of the Laminariales. This indicates that the particularly high UVR sensitivity of zoospores might be a factor determining the vertical distribution of species in the field.

The conclusion of this study is that UVR clearly has the potential to harm Arctic/cold temperate macroalgae. However, several acclimation and protective mechanisms are present in different species to counteract the negative effects. In species from the intertidal or upper sublittoral zone, efficient acclimation mechanisms have evolved to cope with the drastic changes in the ambient light climate. In contrast, algae from the deep sublittoral zone, and therefore generally not exposed to strong UVB, possess only limited capacities for acclimation. However, the knowledge of the species-dependent acclimation potential is not sufficient to predict how the plants will be affected by increasing UVB due to further ozone depletion in future.

ZUSAMMENFASSUNG

Marine Makroalgen der arktischen Region sind starken saisonalen und tageszeitlichen Schwankungen des Strahlungsklimas ausgesetzt. Während des polaren Winters überdauern sie mehr als sechs Monate in Dunkelheit. Im Frühling nach Aufbruch des Meereises sind die Algen erhöhten Bestrahlungsstärken ausgesetzt, insbesondere im klaren Wasser bei Niedrigwasser. Die aus einem stratosphärischen Ozonabbau resultierende erhöhte UVB-Strahlung verstärkt den Strahlungsstress zusätzlich. Das Ziel der vorliegenden Arbeit war es, die möglichen Auswirkungen einer erhöhten UV-Strahlung auf die Physiologie arktisch/kaltgemäßigter Makroalgen in Labor und im Freiland zu untersuchen. Diese Studien sollen als Grundlage dienen, langfristige Vorhersagen zur Entwicklung arktischer Küstenökosysteme im Hinblick auf veränderte UV-Einstrahlungen vorzunehmen.

Die Bestrahlungsbedingungen in der Arktis sind starken saisonalen Schwankungen unterworfen. Im Untersuchungsgebiet (Kongsfjord, Spitzbergen) bei einem Breitengrad von 80° Nord herrscht andauernde Dunkelheit von Mitte Oktober bis Mitte Februar, der Polartag dauert von Mitte April bis Mitte August. Während des Sonnenhöchststands werden dort maximale Strahlungsintensitäten von 1300 µmol Photonen $m^{-2}s^{-1}$ photosynthetisch aktiver Strahlung (PAR; 400-700 nm), 19 Wm^{-2} UVA (320-400 nm) und 1,09 Wm^{-2} UVB (280-320 nm) am Erdboden gemessen. Spektroradiometrische Strahlungsmessungen zeigen, dass die Intensität der UVB-Strahlung dabei stark von der Ozonkonzentration in der Stratosphäre abhängig ist. Das Lichtklima in der Wassersäule ist zudem sehr variabel. Gelöstes organisches Material (DOM), Sediment, Phytoplanktonblüten, aber auch der Tidenverlauf beeinflussen zusätzlich die Bestrahlung von Makroalgen am natürlichen Standort. Die maximale Eindringtiefe von UVB-Strahlung in den Kongsfjord liegt bei ungefähr 10 m.

UVB-Bestrahlung kann verschiedene biologische Prozesse, wie die Photosynthese, schädigen. Das Ausmaß der UV-induzierten Inhibition der Photosynthese, sowie das Anpassungspotential an eine erhöhte UV-Bestrahlung ist artspezifisch. Dies zeigte ein Freilandversuch, in dem Individuen verschiedener Arten in größeren Wassertiefen gesammelt und in geringere Tiefen transplantiert wurden. Typische Arten aus dem oberen Sublitoral (z.B. *Palmaria palmata*) können

sich schnell an die erhöhten Strahlungsbedingungen im Weißlicht und im UV-Bereich anpassen, während die Photosynthese der Arten aus dem unteren Sublitoral (z.B. *Phycodrys rubens, Ptilota plumosa*) schwer geschädigt wird. Diese Versuche belegen, dass unterschiedliche Anpassungsfähigkeiten bei den verschiedenen Arten vorliegen, die durch ein unterschiedliches genetisches Potential bedingt sein müssen.

Verschiedene Prozesse innerhalb der Photosynthese werden durch UV-Strahlung geschädigt. In dieser Studie wurde zum ersten Mal die UV-Empfindlichkeit der Enzyme des Calvin Zyklus, Ribulose-1,5-bisphosphat Carboxylase/Oxygenase (RubisCO) und Glycerinaldehyd-3-phosphat Dehydrogenase (G3PDH) in Makroalgen untersucht. Das Enzym RubisCO reagiert besonders empfindlich auf UV-Bestrahlung. Die beobachtete Reduktion des photosynthetischen Elektronentransports ist auf eine herabgesetzte RubisCO-Aktivität zurückzuführen. Die sinkende Enzymaktivität resultiert aber auch zum Teil aus einem Abbau des Enzyms. An der Braunalge *Alaria esculenta* konnte gezeigt werden, dass sich parallel zur schwindenden Konzentration der großen und kleinen RubisCO-Untereinheit ein Proteinkomplex mit einem höherem Molekulargewicht ausbildet, der vermutlich aus einem Aggregat der abgebauten Enzym-untereinheiten besteht. Im Gegensatz zu RubisCO erweist sich G3PDH als viel resistenter gegenüber UV-Bestrahlung.

Makroalgen müssen im Laufe der Evolution Anpassungsstrategien entwickelt haben, um auf die starken Schwankungen in den Bestrahlungsverhältnissen reagieren zu können. Frühere Studien belegen, dass UV-Strahlung einen hemmenden Einfluss auf die Photosynthese ausübt. Die Braunalgen *Laminaria saccharina, Alaria esculenta* und *Saccorhiza dermatodea* zeigen unter einem simulierten Sonnenspektrum, dass verschiedene Akklimatisationsmechanismen vorhanden sind, die die Photosynthese vor erhöhter UV-Strahlung schützen. Die maximale Quantenausbeute der Photosynthese in Individuen aus größeren Tiefen wird deutlich stärker abgesenkt als bei den Algen derselben Art aus geringeren Wassertiefen. Das bedeutet, dass diese Arten ein Anpassungspotential besitzen, das den einzelnen Arten ermöglicht, einen großen Tiefenbereich zu besiedeln. Der zeitliche Verlauf der Anpassung an erhöhte UV-, aber auch Weißlichtbestrahlung wurde näher an der Braunalge *Alaria esculenta* studiert. An Schwachlicht angepasste Algen wurden unter der Eisdecke im Frühjahr gesammelt und dann im

Labor wiederholt verschiedenen Strahlungsbedingungen ausgesetzt. Es zeigte sich, dass sich diese Art binnen weniger Tage an die künstliche UV-Strahlung anpasst. Während einer ersten Exposition wird die maximale Quantenausbeute der Photosynthese zunächst deutlich inhibiert, und die Alge erholt sich anschließend nur langsam. Während weiterer Expositionszyklen nimmt als erstes die Erholungsgeschwindigkeit zu, später fällt das Ausmaß der UV-induzierten Inhibition auch geringer aus. In Algen, die zuvor an hohe Weißlichtbestrahlung angepasst wurden, führt eine zusätzliche UV-Bestrahlung zu keiner zusätzlichen Inhibition, aber die Erholung der Photosynthese wird verzögert. Dies zeigt, dass die Inhibition der Photosynthese unter natürlichen Strahlungsbedingungen vorwiegend durch Weißlicht induziert wird, während UVR vor allem eine Verzögerung der Erholungsprozesse hervorruft.

In situ-Experimente mit der Braunalge *Laminaria saccharina* und der Rotalge *Palmaria palmata* zeigten, dass die Photosynthese dieser Arten an ihrem natürlichen Standort kaum durch UVB-Bestrahlung beeinträchtigt wird. Bei einer Erhöhung der Bestrahlungsintensität durch Transplantation der Individuen von 3 in 1 m Tiefe, tritt eine schrittweise Anpassung der maximalen Quantenausbeute der Photosynthese auf. Eine zusätzliche künstliche UV-Bestrahlung im Labor wirkt sich anschließend kaum negativ auf die Algen aus, die mehrere Tage zuvor in 1 m Wassertiefe exponiert waren. Im Gegensatz dazu reagieren Proben aus größeren Tiefen sehr empfindlich auf die zusätzliche UV-Bestrahlung.

Ein möglicher Anpassungsmechanismus an erhöhte UV-Strahlung ist die Synthese von UV-absorbierenden Substanzen. In der arktisch endemischen Rotalge *Devaleraea ramentacea* wurde die UV-induzierte Synthese von UV-absorbierenden Mycosporin-ähnlichen Aminosäuren (MAAs) nachgewiesen. Diese Substanzen sind bei Rotalgen aus dem Eulitoral und oberen Sublitoral weit verbreitet und bieten einen teilweisen Schutz der Photosynthese vor UV-bedingter Schädigung. In *D. ramentacea* wird die Synthese von MAAs hauptsächlich durch UVB-Strahlung induziert, dies wurde mittels eines UV-Ausschlussexperimentes im Freiland festgestellt. Die MAA-Konzentration in der Alge wird durch verschiedene Faktoren beeinflusst, die aber alle mit den jeweiligen Bestrahlungsverhältnissen zusammenhängen. So wurden von demselben Standort Proben im Mai und im August gesammelt; am Ende des polaren Sommers gesammelte Proben, enthalten deutlich mehr MAAs, ebenso ist der MAA-Gehalt mit der jeweiligen Tiefe korreliert,

in denen die Algen wachsen. Algen aus geringeren Tiefen enthalten deutlich höhere MAA-Konzentrationen. Auch gibt es einen Konzentrationsgradienten innerhalb eines Thallus. Die strahlungsexponierten Spitzen enthalten höhere MAA-Konzentrationen als die beschattete Basis.

Die Konzentration und Zusammensetzung von MAAs ist artspezifisch. Es ist anzunehmen, dass die Fähigkeit, hohe Konzentrationen an MAAs zu akkumulieren, eng mit dem jeweiligen Standort einer Art im Zusammenhang steht. Unter diesem Aspekt wurden auf Helgoland die beiden nah verwandten Rotalgen *Chondrus crispus* und *Mastocarpus stellatus* untersucht. Proben beider Arten wurden von demselben Standort gesammelt und im Labor künstlicher UV-Strahlung ausgesetzt. Die Photosynthese von *C. crispus* reagiert deutlich sensibler auf UV-Strahlung als die von *M. stellatus*. Ein Grund dafür könnte die stark unterschiedliche Ausstattung mit MAAs in beiden Arten sein: *M. stellatus* enthält bis zu 6 mal mehr MAAs pro Gramm Trockengewicht als *C. crispus*. Dies könnte es *M. stellatus* ermöglichen, stärker sonnenexponierte Flächen zu besiedeln.

Unterschiedliche Entwicklungsstadien unterscheiden sich in ihrer jeweiligen UV-Toleranz. Dies zeigt die Reaktion der Zoosporen von Braunalgen. Die Photosynthese der Sporen reagiert viel empfindlicher auf UV-Strahlung als die der Sporophyten. UV-Bestrahlung kann zum Absterben der Sporen führen. Sporen verschiedener Braunalgen aus der Arktis und aus Südspanien wurden denselben UV-Dosen ausgesetzt. Die Überlebensrate nach Exposition ist artspezifisch. Generell sind die Sporen von Arten, die das untere Sublitoral besiedeln (z.B. *Laminaria saccharina*), empfindlicher als Sporen von Arten, die im oberen Sublitoral wachsen (z.B. *Chordaria flagelliformis*). Bei *Laminaria digitata* ist die UV-induzierte Mortalität der Sporen mit der Zahl der gebildeten Thymin-Dimere in der DNA, d.h. mit einer Schädigung der DNA korreliert. In Südspanien sind die UV-Intensitäten in Wassertiefen bis 7 m so hoch, dass sie zum Absterben der Sporen von Arten der Ordnung Laminariales führen. Die Ergebnisse zeigen, dass Sporen ein besonders UV-sensitives Entwicklungsstadium darstellen und dass diese UV-Empfindlichkeit die Vertikalzonierung der Arten am natürlichen Standort beeinflusst.

In der vorliegenden Arbeit wird deutlich die potentiell schädigende Wirkung einer erhöhten UV-Strahlung auf die Photosynthese arktisch/kalt-gemäßigter Makroalgen demonstriert. Allerdings können die Algen durch verschiedene Anpassungs- und Schutzmechanismen den schädigenden Effekten teilweise

entgegenwirken. Arten des Eulitorals und des oberen Sublitorals verfügen über effiziente Akklimatisationsstrategien, mit denen sie auf die extremen Schwankungen im Bestrahlungsklima am natürlichen Standort reagieren. Algen aus dem unteren Sublitoral hingegen verfügen nur über geringe Anpassungsmöglichkeiten. Andererseits sind diese Arten an ihrem Standort aufgrund der geringen UV-Transmission niemals hohen UV-Intensitäten ausgesetzt. Über das artspezifische Anpassungspotential ist bisher noch zuwenig bekannt, um vorauszusagen, in welchem Ausmaß Makroalgen von einer Erhöhung der UVB-Strahlung durch weiteren Ozonabbau betroffen sind.

1. INTRODUCTION

1.1. General introduction

Solar radiation is the most important prerequisite for life on earth. In the process of photosynthesis, photoautotrophic organisms 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 promote photosynthesis, but can also inhibit many biological processes if radiation becomes excessive, or if short wavelength radiation with a high energy content is absorbed by biomolecules. Consequently, damage to important components of plant metabolism does result in reduced photosynthetic and general metabolic activity and, hence, leads to a decrease in biomass production. Ever since the discovery of the Antarctic ozone hole 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). Recent research indicates that thinning of the stratospheric ozone layer is becoming more serious also over the polar regions of the Northern hemisphere (Jokela et al. 1993; Müller et al. 1997; Rex et al. 1997). In the Arctic, low light adapted organisms may react particularly sensitive to alterations in the solar spectrum (Kirst and Wiencke 1995).

As the Arctic aquatic ecosystem is regarded as one of the most productive areas on earth (Springer and McRoy 1993; Orheim et al. 1995), intensive research has been directed towards the interaction of the changing irradiance regime and other abiotic parameters, and the response of marine macroalgae as key organisms within the Arctic coastal ecosystem. The study presented here formed part of an international project funded by the European Community, directed to elucidate the effects of ultraviolet radiation (UVR) on marine macrophytes along a latitudinal gradient from the Arctic to the warm temperate regions of Southern Spain. As information on the effects of UVR on the physiology and ecology of Arctic marine macroalgae is still scarce, this thesis was formulated to answer the following questions:

- How does macroalgal photosynthesis respond to UVR exposure and what are the basic physiological mechanisms?
- How do presently observed UVR levels affect Arctic macroalgae in the field?
- How do macroalgae acclimate to the strong changes in light climate at their natural growth site?
- Is solar UVR a factor determining macroalgal depth zonation in the field?

1.2. Ozone depletion and UV radiation

Early evidence for the seasonal development of a so called „ozone hole" over Antarctica was gathered in the early 1970´s (Farman et al. 1985). The expression „ozone hole" is used whenever normal average ozone concentration drops below 50%. The concentration of stratospheric ozone (O_3) is expressed in Dobson units (DU); normal summer values are about 400 DU over the polar regions of both hemispheres (Heese 1996). Ozone is predominantly generated in the low latitudes, by photolysis of molecular oxygen. As ozone production rate is strongly dependent on the concentration of molecular oxygen, as well as solar irradiance, ozone formation occurs mainly in tropical regions. In the stratosphere, ozone molecules are subject to UVR-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 increase mainly in the atmosphere due to anthropogenic emissions, thus leading to ozone depletion. In the Arctic, seasonal O_3 depletion is enhanced during long term exposure to very low temperatures as documented for winter/spring 95/96 and 96/97. These conditions promote the formation of so called polar stratospheric clouds (PSC), containing high concentrations of chlorine and nitrogen, leading to the destruction of O_3-molecules (Müller et al. 1997; Rex et al. 1997).

Ultraviolet radiation includes the wavelengths below those visible for the human eye. This spectral range is divided into three wavebands which are defined as follows: 320-400 nm UVA, 280-320 nm UVB, and 190-280 nm UVC,

which does not occur as a natural part of the solar spectrum on the earth´s surface, as it is completely absorbed on its way through the atmosphere. The potential danger of UVR derives from its high energy content according to the Planck equation:

$$E = h \cdot (c \cdot \lambda^{-1})$$

with the respective energy content E, the Planck constant h, the speed of light c at wavelength λ. 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).

1.3. General biological effects of UVB radiation

The effects of UVB exposure on biological systems are manifold, and reach from the molecular to the organismic level, thereby affecting growth and production, and, consequently, ecosystem structure and function. A prerequisite for UVB induced damage is the UVR absorption by biomolecules. Potential UVR chromophores in plants mainly include nucleic acids (such as DNA, RNA) and proteins (Vass 1997). These biological compounds play a key role in the structure and function of plant cells, therefore any UVR induced alteration of these compounds can result in physiological alterations within the plant.

UVR induced DNA damage occurs directly by the absorption of UVB quanta by aromatic residues. The results are structural alterations such as formation of cyclobutane dimers (single strand breaks) and pyrimidine (6-4)-pyrimidone (6-4)-photoproducts (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 UVR absorption. A review on UVB induced lesions of the DNA is given by Mitchell and Karentz (1993). UVR 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 UVR in organisms. Furthermore, disulphide bonds between cysteine residues in the protein can be split 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 also be destroyed by UVR 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 UVR 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).

On the organismic level, the above mentioned molecular effects can result in reduced growth and production, as shown in higher plants, phytoplankton and ice algae (Caldwell 1971; Worrest 1983; Ekelund 1990; Karentz et al. 1991; Holm-Hansen 1993a, b; McMinn et al. 1999). Conclusive information on the effects of UVR on growth of marine macroalgae has only recently become available (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 (Wiencke et al. 2000). Consequently, all aspects mentioned may also affect ecosystem structures (Holm-Hansen et al. 1993; Johanson et al. 1995a; Caldwell et al. 1998).

1.4. Inhibition of photosynthesis

1.4.1. *UVR induced photoinhibition*

Photosynthesis may be 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 biomolecules involved in photosynthesis, the effects of UVR exposure are manifold (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 PS I is only minimally affected by UVB (by inhibiting PS I-mediated cyclic photophosphorylation; Iwanzik et al. 1983; Renger et al. 1986), 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. This may be due to interactions with the electron transfer from phaeophytin to plastoquinone or by directly affecting the plastoquinones Q_A and Q_B, both of which absorb strongly in the UVB region (Iwanzik et al. 1983). Therefore, UVR may cause structural modification of the Q_A and Q_B apoproteins. Furthermore, the function of the D_1 protein may be impaired by the UVB induced fragmentation of the protein (Renger et al 1989; 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. 1989). 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). In addition to the direct damage to PS II, structural disturbance to membranes is likely to result in a reduced photosynthetic activity, e.g. due to dilation of the thylakoid membranes and rupture of the chloroplast double membrane (Iwanzik et al. 1983; Strid et al. 1994). 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).

Recently, the CO_2-fixing enzyme RubisCO has been shown to be another critical component in UVR induced inhibition of photosynthesis. The UVR 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). Another effect of UVB on reactions related to photosynthesis represents the inactivation of chloroplast ATPase (Strid et al. 1990). Impairment of any of the above mentioned components can contribute to lower the photosynthetic activity during and following UVR exposure.

1.4.2. *Photoinhibition induced by photosynthetically active radiation (PAR)*

Reduced photosynthetic activity has also been observed in plants exposed to high PAR, occurring as soon as light exposure exceeds the demands of photosynthesis; originally, this effect was termed photoinhibition. In the field, harmful UVB radiation is generally accompanied by high irradiances of PAR. Although the measurable effects, such as e.g. reduced photosynthetic efficiency, are similar, the mechanisms behind UVR and PAR induced inhibition of photosynthesis are very different, therefore both events should be carefully distinguished (Neale et al. 1993).

The different mechanisms involved in PAR induced photoinhibition are briefly described in the following. Exposure to high irradiances of PAR can exceed the assimilatory capacity of the Calvin cycle (Ruban and Horton 1994), then excessively absorbed energy may consequently result in damage to the photosynthetic apparatus. Under conditions of a high reduction state of ferredoxin, electrons transferred from PS I to oxygen can generate superoxide radicals (Mehler reaction). Reactive oxygen species (ROS) can oxidise chlorophylls and proteins, for instance, the D_1 protein in the reaction centre of PS II (Andersson et al. 1992). The D_1 protein undergoes a permanent turnover cycle of synthesis, degradation and replacement in the thylakoid membrane. As soon as the rate of damage exceeds the rate of repair, the function of the

reaction centre is impaired and the final consequence is the destruction of the photosynthetic apparatus (Aro et al. 1993). To protect photosynthesis from high irradiances of PAR, plants do activate different mechanisms. The increase of thermal dissipation removes excessively absorbed energy before the generation of ROS occurs. The mechanism behind this is proposed to include an increase in heat dissipation within the antennae by the interconversion of violaxanthin to zeaxanthin within the xanthophyll cycle, which is also described for green and brown algae (Demmig-Adams 1990; Uhrmacher et al. 1995; Schofield et al. 1998). Zeaxanthin may act as a direct quencher of excited triplet chlorophyll, thus avoiding energy transfer to triplet oxygen (Frank et al. 1994). ROS may be quenched by carotenoids and other antioxidants (as e.g. glutathion), or they may be enzymatically degraded by superoxide dismutase (SOD), catalase or peroxidase (Barber and Andersson 1992; Asada and Takahashi 1987). However, if light stress exceeds the protective capacity, damage to the photosynthetic apparatus occurs, and plants do bleach due to the photooxidation of pigments (Björkman 1981; Krause 1988).

In order to distinguish it from photodamage, the term photoinhibition is defined in recent times as a regulatory mechanism (Krause and Weis 1991). Osmond (1994) makes a further distinction between the terms dynamic and chronic photoinhibition. During dynamic photoinhibition, excessively absorbed energy is harmlessly dissipated as heat, thereby lowering quantum yield and thus photosynthetic efficiency (Krause and Weis 1991). This process is regarded as a protective mechanism to prevent generation of excited triplet chlorophylls and hydroxyl radicals. After the offset of stressful conditions, the plant is able to recover rapidly from dynamic photoinhibition, and increase its quantum efficiency again. In contrast, during chronic photoinhibition, photosynthetic capacity is mainly affected by the impairment of the D_1 protein. Due to the required *de novo*-synthesis and the replacement of damaged D_1 protein in the thylakoid membrane, this effect is only reversible on a longer time scale (Mattoo et al. 1984).

In contrast to PAR, UVR can not be regarded as being "excessive" in a proper sense. As pointed out earlier, it exhibits adverse effects on photosynthesis in a more direct way, such as its absorption by biomolecules.

The high potential of UVR to inhibit photosynthesis was firstly demonstrated by Jones and Kok (1966). Whilst within the PAR region, the action spectrum of photoinhibition runs in parallel with the action spectrum of photosynthesis, and is therefore related to photosynthetic pigment absorption, UVB induced inhibition is related to its absorption by DNA and proteins, conversely (Jones and Kok 1966; Setlow 1974). However, as described in the following section, several mechanisms for protection against those harmful wavelengths have evolved in plants.

1.5 Adaptive strategies

Plants have developed numerous strategies to reduce the damaging impact of UVR. During acclimation to changing radiation conditions, UVR screening compounds are formed to protect the photosynthetic apparatus against the harmful radiation, thereby shielding critical cellular components (Karentz 1994; Helbling et al 1994). UVR screening compounds include flavonoids and anthocyans in higher plants (Teramura and Sullivan 1994; Day et al. 1992), as well as carotenoids, coumarins and phenolic compounds which also occur in algae (Pavia et al. 1997; Götz et al. 1999; Pérez-Rodríguez et al. 1998). Another group of UVR screening substances are mycosporine-like amino acids (MAAs), which have been shown to have a wide distribution among marine organisms (Dunlap and Shick 1998; Karsten et al. 1998; Sinha et al. 1998). These water soluble compounds are characterised by a cyclohexenone or cycloheximine ring conjugated with the nitrogen substituent of an amino acid or its imino alcohol, exhibiting absorption maxima in the range of 310-360 nm, and an average molecular weight of approximately 300 dalton (Dunlap and Shick 1998).

MAAs have been identified in a number of taxonomically diverse organisms such as fungi, a marine heterotrophic bacterium, cyanobacteria, eucaryotic algae, marine invertebrates, fish and other marine organisms (Sinha et al. 1998). The MAAs are algal, bacterial or fungal products of the shikimic acid pathway, not present in animals. However, marine consumers may benefit

from the UVR protective role of these compounds by feeding on a diet containing MAAs and accumulating these in their own tissue (Adams and Shick 1996). MAAs are also frequently found in red algae from polar to tropical regions (Karsten et al. 1998a, b).

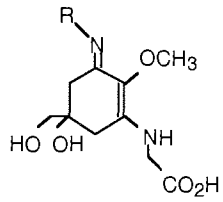

Fig. 1: General molecular structure of mycosporine-like amino acids; R = different residues.

Another adaptive strategy is the fast repair of UVR mediated DNA damage. Generally, two different mechanisms of enzymatic DNA repair occur. (1) The photoreactivation by photolyase is a rapid process leading to the monomerisation of dimers formed by UVB absorption (photorepair), this needs sufficient radiation levels to be active (Lois and Buchanan 1994). (2) The second process involved is called excision repair, where damaged parts of the DNA are enzymatically removed by cutting them out of the molecule; this slow process is light independent (Stapleton 1992).

The establishment of an antioxidative protection system against harmful ROS is another effective process involved in lowering the negative effects of UVB radiation. Carotenoids, flavonoids and other antioxidants, such as ascorbate and glutathion, act as potential radical quencher in plants. Furthermore, enzymatic antioxidant systems are efficiently detoxificating ROS by the activity of catalase, SOD, and peroxidase (Asada and Takahashi 1987).

Generally, the establishment of any kind of adaptive strategy requires additional energy costs. Consequently, effective protection of photosynthesis can result in lowered photoinhibition but also in reduced growth rates.

1.6. UVR and macroalgae in Arctic coastal ecosystems

The effects of UVR on aquatic ecosystems are strongly dependent on the optical properties of the water body. Under ozone depleted conditions, biological relevant irradiances of UVB have been recorded in 30 m depth in Antarctica (Karentz 1989; Vosjan et al. 1996). In very transparent waters UVB can even be detected down to 65 m depth (Smith et al. 1992).

However, due to the wavelength dependent absorption in the water column and in the presence of high concentrations of dissolved organic matter (DOM), often characteristic for coastal waters, UVB radiation does generally not penetrate deeply into the water body (Jerlov 1976; Kirk 1994). Several factors affect the degree of UVR exposure of aquatic organisms. 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 strongly influenced, by tidal action, water turbidity (sediment), phytoplankton blooms, sea ice and snow cover, plant canopies and, as already mentioned, by DOM (Häder et al. 1998; Hanelt et al. 2000a).

There are some important peculiarities in abiotic factors with respect to how Arctic coastal ecosystems differ from temperate as well as Antarctic regions. Generally, the Arctic coastal environment is characterised by low temperatures, long periods of ice and snow cover and pronounced seasonal variations of temperature and salinity, and most drastically, in the light period. At 80° North the polar day lasts from mid of April to the middle of August, and the polar night from the middle of October to the middle of February. Furthermore, sea ice cover, which still can persist during Arctic spring confers a strong seasonal impact on exposure of marine organisms to solar radiation (Mehlum 1991; Ito and Kudoh 1997; Vincent et al. 1998). Consequently, as a result of the long polar night and prolonged sea ice and snow cover, Arctic macroalgae endure about 6 months of darkness and are suddenly exposed to high solar radiation as soon as the ice cover breaks up in early summer (Bischof et al. 1999; Hanelt et al. 2000a). In contrast to Antarctic waters, the Arctic ocean

represents a virtually closed water mass with a very limited water exchange and receives about 10% of the world river discharge (Hempel 1987). The freshwater inflow results in a stratification of the water masses and is responsible for the input of large fractions of sediment, thus strongly reducing UVR transmittance (Wängberg et al. 1996). This is a pronounced seasonal effect, as turbid freshwater discharge is a result of snow melting and the calving of glaciers in summer (Hanelt et al. 2000a).

In most coastal ecosystems, marine macroalgae play a major role as key organisms. As primary producers they represent the basis of the food chain and provide food for herbi- and detrivores (Dunton and Schell 1987; Iken 1996; Iken et al. 1997). They serve as shelter for a number of motile and sessile organisms (such as crustaceans, juvenile fish, etc.) and serve as substrate for a large variety of epiphytes (Klöser et al. 1996; Klöser 1998). Therefore, damage to the macroalgal community is likely to have serious consequences for the whole coastal ecosystem.

The degree of exposure of macroalgae to high radiation is strongly dependent on the respective growth depth of the specimen. Eulittoral algae (e.g. *Fucus* sp.) are fully exposed to high solar radiation at low tide and therefore need to develop strategies to cope with the high radiation. More shade adapted species either grow in the sublittoral zone (and are thus protected against high radiation by the water column above), or they grow as subcanopy species being shielded by other algae. Typical low light adapted species along the Arctic coastline are *Laminaria solidungula, Phycodrys rubens, Ptilota plumosa*. Polar species exhibit some ecological peculiarities, which enable them to prevail under the harsh conditions, e.g. low temperatures, freezing, seasonal changes of high and low irradiance (see Kirst and Wiencke 1995 for review). Even during the polar summer, the highest sun position is low compared to the lower latitudes. During winter and under ice and snow cover, algae are also exposed to darkness for several months. Therefore, polar macroalgae are generally considered to be low light adapted (Kirst and Wiencke 1995). Physiology as well as the whole life-cycle of polar algae (growth and reproduction) is synchronised to the seasonal changes in this unique environment (Chapman and Lindley 1980; Dunton 1985, 1990; Dunton

and Schell 1986; Gómez et 1995a, b). The specific biological features, maintaining Arctic macroalgal productivity can be summarised by three factors: (1) the high efficiency of light utilisation, (2) adaptation to low temperature, and (3) significantly reduced rates of respiration at low temperatures (Dunton and Dayton 1995).

In many Arctic species, the time of maximal growth coincides with a period of maximal water transparency in spring/early summer (Chapman and Lindley 1980). Solar radiation also reaches its maximum levels during these times. Consequently, harmful UVB radiation may penetrate deeply into the coastal water, and the question arises whether a further increase of UVB radiation on the earth's surface may result in an impairment of macroalgal physiology, thus affecting growth and the ecosystem function.

1.7. Thesis outline

During the last years, a steadily increasing number of studies has been directed to investigate the potential effects of UVB exposure on plant life. Due to the economic significance, the most detailed studies were hitherto performed on crop plants (see Fiscus and Booker 1995 for review). In contrast, information on UVR effects on marine macroalgae are still scarce, and this is particularly valid for polar species. As the most drastic ozone depletion is observed over the polar regions of both hemispheres, and due to the central role of macroalgae in the Arctic coastal ecosystem, such studies were urgently needed.

As indicated above, the UVR effects on marine macroalgae are far too numerous to be completely illustrated within only one study. This synopsis summarises nine original research papers, each directed to study different aspects involved in the response of marine macroalgae to UVR, and one review article. However, this study can only focus on a few key questions within the broad topic of UVR research. In the following, a brief description of the content of the respective publications is given:

The study by Hanelt et al. (2000a) focuses on the detailed description of radiation conditions at the Arctic study site, where most of the practical work has been performed, but is also of general interest as it provides a fundamental basis for UVR research in Arctic coastal ecosystems.

A central topic in an ecological context is the adaptive response to the predicted changes in the radiation conditions. As Arctic macroalgae experience strong seasonal and also daily variations in light climate, this point is of general interest in respect to species ecology, and therefore, it represents a major part within this study. Bischof et al. (1998b) show that photosynthesis is particularly acclimated to the radiation climate of PAR and UVR at the respective growth depth of the specimen. Another study (Bischof et al. 1999) focuses on the time scale required for adjustment of photosynthetic response to the strong variations in light climate for one ecological important species. The article by Brouwer et al. (2000) deals with an *in situ* experiment. This is of particular importance for clarifying the ecological significance of UVR exposure under field conditions. In a study by Karsten et al. (2000), the species dependent sensitivity of photosynthesis to solar radiation was investigated under field conditions.

The impact of UVR on macroalgal zonation patterns has also been addressed in the work by Wiencke et al. (2000). Here, the UVR sensitivity of brown algal zoospores and the possible consequences for depth zonation of species was investigated.

The protection of algal photosynthesis by the formation of internal UVR screening compounds is another central topic within this study. Karsten et al. (1999) describe field experiments conducted on an Arctic endemic red algal species, and provide conclusive data for the MAA mediated protection of photosynthesis against UVR. The experiments presented by Bischof et al. (2000b) were conducted on the island of Helgoland, Germany. The main question to answer was to what extent the different composition of MAAs and different sensitivities of photosynthesis to UVR may contribute to the vertical distribution of two closely related red algal species on the shore.

The activity of RubisCO in higher plants was shown to be strongly impaired by UVR; the study by Bischof et al. (2000a) follows a physiological

approach and describes the effect on photosynthetic dark reactions during exposure of marine macroalgae to UVR, which has never been investigated before.

A review article by Bischof et al. (2000c) summarises the current state of knowledge on UVR effects on Arctic marine macroalgae.

2. METHODOLOGICAL ASPECTS

In the following, a brief overview on particular techniques applied within this study is given. For further details on sampling, cultivation and processing of samples, as well as on the respective experimental protocols, equipment used and standard procedures, such as determination of chlorophyll content, the reader is referred to the Material and Methods section within the respective publications.

2.1. Irradiance applied

All experiments conducted in the framework of this thesis were designed to study radiation effects on macroalgal physiology. In the context of elevated UVB levels, the physiological effects of different wavelength ranges had to be separated. Throughout all experiments the experimental individuals were covered with various glass filters or filter foils cutting off different spectral ranges from the light spectrum applied. In field experiments (Brouwer et al. 2000; Karsten et al. 1999, 2000), the samples were exposed to solar radiation, thus the experimental dose was predominantly dependent on the prevailing weather conditions (Hanelt et al. 2000a). In the laboratory (Bischof et al. 1998b, 1999, 2000a, b; Wiencke et al. 2000), special fluorescent tubes (UVA 340, Q-Panel, USA) were used, emitting a spectrum below 340 nm similar to the solar one. Spectral irradiances of the UVR and PAR range, and the effect of the cut-off filters used are illustrated in Fig. 2.

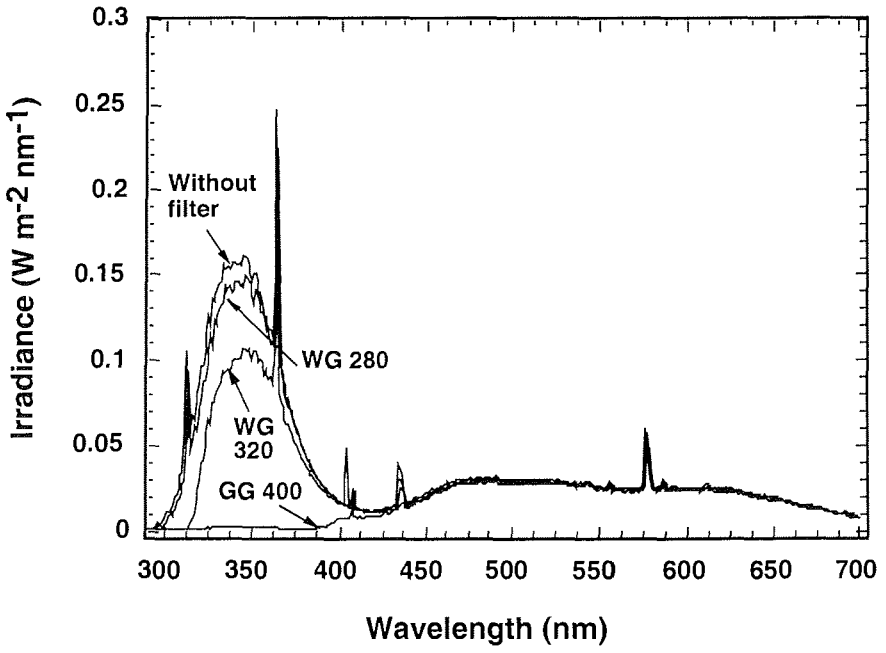

Fig. 2: Spectral irradiance of UVR (290-400 nm) and PAR (400-700 nm) emitted by Q-Panel UVA-340 fluorescent tubes and the effects of cut-off filters (Schott) used in the experiments. WG 280 = PAR + UVA+ UVB; WG 320 = PAR + UVA; GG 400 = PAR alone. Redrawn from Wiencke et al. (2000).

2.2. Measurements of photosynthesis

The effects of UVR on the overall photosynthetic activity has been assessed by measuring the emission of variable chlorophyll fluorescence of PS II with the pulse-amplitude modulated fluorometer PAM 2000 (Walz, Germany). The physiological basis of this technique is reviewed by Krause and Weis (1991) and Schreiber et al. (1994). Maximal quantum yield of photosynthesis, reflecting mainly the efficiency of energy transfer from the antennae to the reaction centre was measured by the ratio of variable to maximal fluorescence (Fv/Fm). The exact determination of this parameter in different species of Arctic macroalgae is described in detail by Hanelt (1998).

To estimate overall photosynthetic capacity, maximal relative electron transport rates (ETRmax) were calculated from fluorometrically monitored photosynthesis *vs.* irradiance curves (PI-curves), according to Schreiber et al.

(1994). PI-curves were recorded by measuring effective quantum yield of PS II ($\Delta F/Fm'$) during a stepwise increase of actinic irradiance at 650±5 nm. Details are given in Bischof et al. 1998b, 1999, 2000a.

The applications and limitations of chlorophyll fluorescence measurements as a means to monitor photosynthetic activity and to detect UVR stress in algae are discussed in section 4.1.1

2.3 Analysis of Calvin cycle enzymes

2.3.1. *Photometric enzyme assays*

The UVR induced changes in the activity of the two Calvin cycle enzymes ribulose-1,5-bisphosphate carboxylase/oxygenase (RubisCO) and glyceraldehyde-3-phosphate dehydrogenase (G3PDH) in crude extracts were studied with a coupled photometric test according to Gerard and Driscoll (1996). Preparation of crude extracts is described in detail by Bischof et al. (2000a).

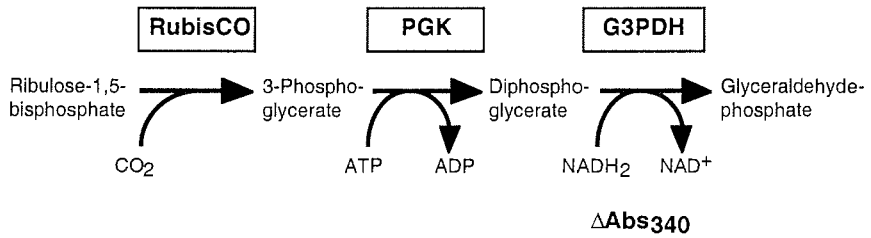

Fig. 3: Simplified scheme of photometric assays of RubisCO and G3PDH activity.

Activity of RubisCO was determined as follows (see Fig. 3): A commercially obtained mixture of G3PDH and phosphoglycerate kinase (PGK; G 8505, Sigma, Germany) was added to the assay mixture, as described by Bischof et al. (2000a). The initial reaction was started by adding ribulose-1,5-bisphosphate as substrate of RubisCO. Consequently, generated 3-phosphoglycerate is converted into diphosphoglycerate by PGK. Finally, the

G3PDH mediated conversion of diphosphoglycerate to glyceraldehyde-3-phosphate is linked with the oxidation of $NADH_2$. The time course of $NADH_2$ oxidation was recorded by the decrease in absorbance at 340 nm. The activity of G3PDH was determined in the same way, but only PGK (P 7634, Sigma, Germany) was added to the assay mixture, and the reaction was started by adding 3-phosphoglycerate. For both enzymes tested, the results obtained were expressed as declining absorbance per mg of total protein per second. Protein content was determined using a commercial Protein Assay (Bio Rad, USA); extinction at 595 nm was measured photometrically and the concentration of proteins was calculated according to a calibration curve prepared with known concentrations of bovine serum albumine. Further details are given by Bischof et al. (2000a). For comments on the application and limitations of the described test, readers are referred to section 4.1.2

2.3.2. *Sodiumdodecylsulphate polyacrylamide gelelectrophoresis (SDS-PAGE)*

The same crude extracts for determining enzyme activities were used to study changes in RubisCO content. Proteins in the extracts were separated by SDS-PAGE as originally described by Laemmli (1970). All lanes of gels were loaded with an equal amount of protein, to compare alterations in the abundance of specific proteins. Large and small subunits of RubisCO were identified by comparison with gels loaded with commercially obtained isolated RubisCO from spinach (R 8000, Sigma, Germany), and with a molecular weight marker (Rainbow Marker RPN 756, Amersham, UK). Gels were stained with a Coomassie G-250 dye (Merck, Germany) and subsequently scanned with a GS-700 densitometer (Bio Rad, USA). Differences in the abundance of RubisCO in samples exposed to different doses of UVR were analysed with an image analysis software (Multi-Analyst, Bio Rad, USA). Further details on the processing of the gels are given by Bischof et al. (2000a).

3. SUMMARY OF RESULTS

3.1. Radiation climate in the Arctic

Information on the present UVR irradiances in Arctic coastal ecosystems is still very limited. Therefore, a major point of this study was to provide data on the radiation climate at the study site, the Kongsfjord at the North Western coast of Spitsbergen (Fig. 4), and to characterise the macroalgal environment.

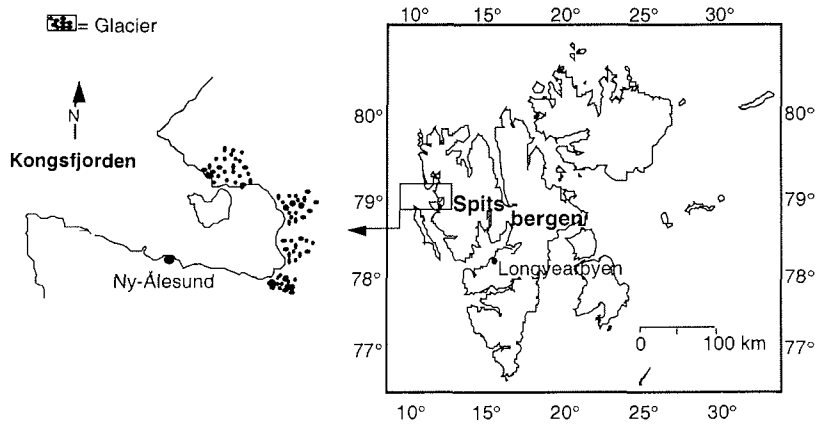

Fig. 4: General view of Spitsbergen and the location of Kongsfjorden. Figure redrawn from Hanelt et al. (2000a).

3.1.1. *Surface radiation*

Light climate in the high latitudes undergoes strong seasonal changes. At the study site, at 79° North, the polar day lasts from the 21st of April to the 22nd of August. From the 26th of October to the 14th of February the sun stays below the horizon during the polar night. Even in summer, when the solar declination is maximal, total irradiance in the atmosphere is comparatively low due to the low angle of the sun (max. 35°) in the high latitudes. Generally, weather conditions at the study site are frequently unstable as shown by the recorded sunshine duration and daily averaged solar irradiance in the course of 3 years (Hanelt et al. 2000a; Brouwer et al. 2000). Maximal irradiance always occur

during June and July, due to the higher solar angle. In June 1997, maximal irradiance of 1300 μmol m^{-2} s^{-1} PAR was recorded at ground level. In parallel, 19 W m^{-2} UVA (320-400 nm) and 1.09 W m^{-2} UVB (280-320 nm) were measured (Bischof et al. 1998b). Under these conditions, a maximal daily fluence of UVB of about 23 kJ m^{-2} was recorded (Hanelt et al. 2000a). Even under high irradiance, no radiation below 300 nm could be detected at ground level at the Arctic study site (Bischof et al. 1998b; Karsten et al. 1999). Spectrometric radiation measurements reveal that UVB irradiances strongly depend on the actual ozone concentration in the atmosphere. By relating irradiance at 300 nm to the irradiance at 320 nm, a so called ozone index has been calculated (see Fig. 5): total atmospheric ozone concentration (data deriving from the total ozone mapping spectroradiometer; TOMS) and the calculated ozone index are negatively correlated (Hanelt et al. 2000a). This allows estimating actual ozone concentration by spectrometrically measured UVB.

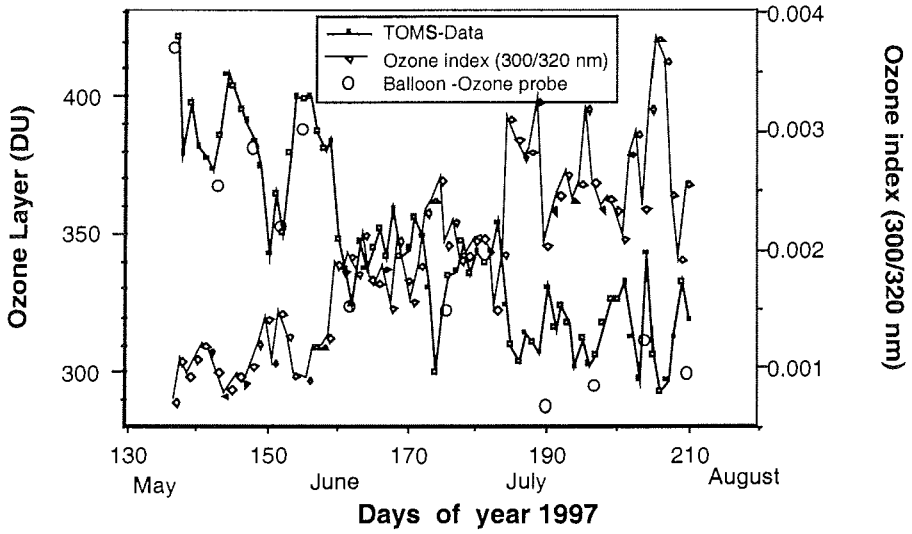

Fig. 5: Total atmospheric ozone concentration (Dobson units, DU) determined with a balloon carried ozone probe, TOMS satellite data above Ny Ålesund, and calculated ozone index as determined by spectroradiometrical measurements from the NDSC-Station (Network for Detection of Stratospheric Changes, Koldewey Station, Alfred Wegener Institute) at Ny Ålesund. Figure redrawn from Hanelt et al. (2000a).

3.1.2. *Underwater radiation*

The radiation climate in the water column was characterised by the use of underwater light sensors and an underwater spectroradiometer. From parallel measurements at different water depths, vertical attenuation coefficients of downward irradiance (K_d) were calculated according to the formula:

$$K_d = 1/(z_2-z_1) \cdot \ln(E_1/E_2)$$

with E_1 and E_2 as the respective irradiance in the depths z_1 and z_2. A low K_d-value of 0.1 m^{-1} corresponds to about 10% light attenuation per meter, a value of 1 m^{-1} indicates about 63% light attenuation per meter in turbid water. Seasonal changes in water turbidity were monitored, showing that transmittance significantly decreases with rising temperatures in summer, melting of snow and calving of glaciers, leading to a large melt water discharge into the fjord (Hanelt et al. 2000a; Brouwer et al. 2000). Due to the absorption chracteristics of natural waters, K_d-values determined for UVA and UVB are generally higher than those determined for PAR (Hanelt et al. 2000a). In 1997, under condition of high water transparency, the 1% depth for PAR was determined to be at 24 m depth, corresponding to a K_d-value of about 0,19 m^{-1}. Later in summer, when water transmittance was reduced, the 1% depth was located at 6 m (K_d=0,74 m^{-1}). Corresponding values for UVB were 9 m (K_d=0,51 m^{-1}) in transparent and 3 m (K_d=1,34 m^{-1}) in turbid waters (Bischof et al. 1998b). The seasonal input of large fractions of sediment and organic material does selectively increase absorption in the short wavelength range. Consequently, attenuation, especially of UVB, is highly variable (Hanelt et al. 2000a). Under conditions of high water turbidity, UVB is not likely to penetrate more than a few centimetres (Fig. 6). Input of freshwater from melting snow results in a stratification of the water column, with a layer of turbid freshwater covering the more transparent water of higher salinity (Hanelt et al. 2000a).

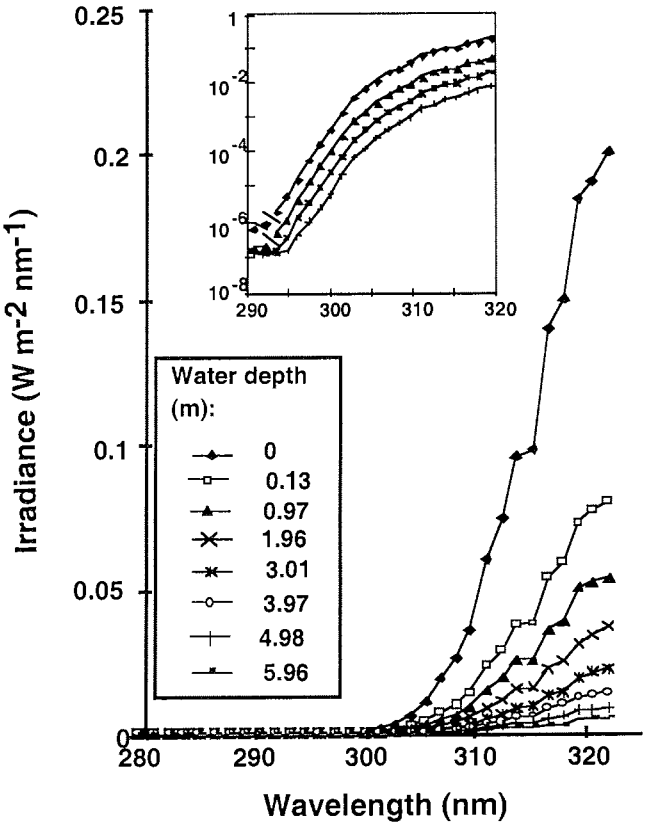

Fig. 6: UVB radiation in the water column of the Kongsfjord (Ny Ålesund), measured on June 15th, 1997; 12:00 local time. Inset shows the radiation at 0, 0.97, 3.01, and 4.98 m depth with a logarithmic scale. Figure redrawn from Bischof et al. (1998b).

Another aspect with a significant seasonal influence on underwater radiation climate is the distribution of sea ice. In the Kongsfjord, a sea ice and snow cover can persist until mid June, thus significantly reducing the incident radiation in the water column (Bischof et al. 1999; Hanelt et al. 2000a).

Apart from seasonal changes in light climate, there is also a marked daily variation of under water radiation. Tidal action results in changing the impinging radiation either by the height of the respective water column or by establishing a stratified water column, consisting of layers of different optical properties (Hanelt et al. 2000a; Fig. 7).

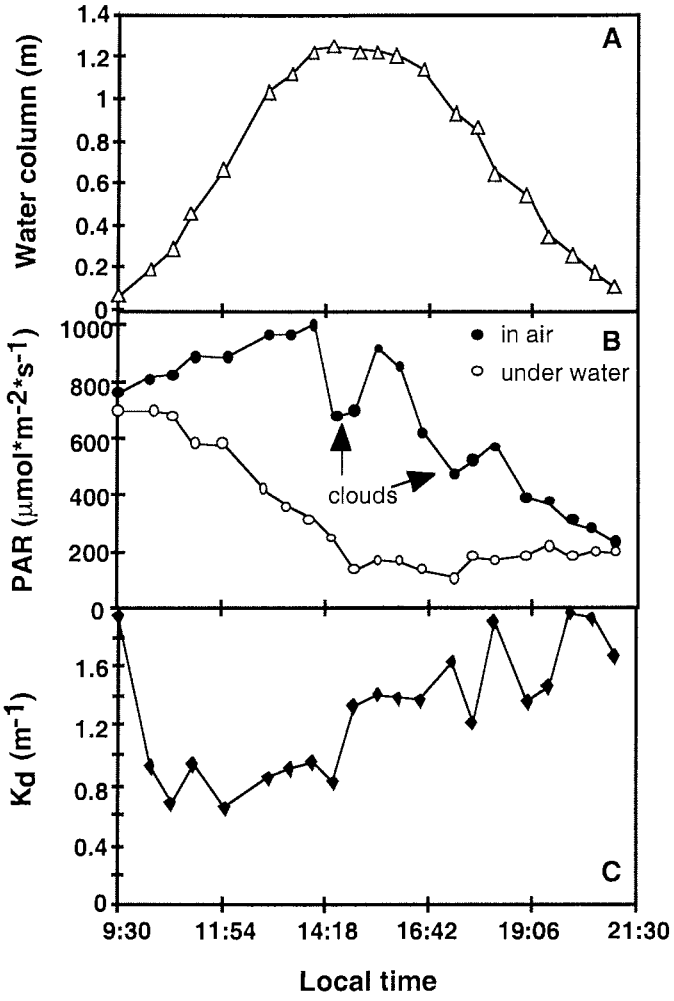

Fig. 7: Dependence of the PAR irradiance and vertical attenuation coefficient (K_d) on the height of the water column in shallow waters of the Kongsfjord, close to Ny Ålesund. A) tidal changes of the water column in the course of July 24th, 1998; B) irradiance in air close to the water surface (●) and at the bottom (O); C) vertical attenuation coefficient (K_d) of PAR inside the water column shown in A. Figure redrawn from Hanelt et al. (2000a).

3.2. Acclimation to changing radiation conditions

3.2.1. *UVR effects on photosynthesis - laboratory experiments*

Due to the drastic changes in light climate at the respective growth site, marine macroalgae must be able to acclimate and adjust photosynthesis to the various radiation conditions. The differential sensitivity of the photosynthetic process to UVR in relation to the original growth depth of specimens was studied in the brown alga *Laminaria saccharina* (Bischof et al. 1998b). Samples, collected at 3, 6, 11, 14 m water depth, were exposed to the same dose of artificial UVR. Both, maximal quantum yield of photosynthesis (Fv/Fm) as well as maximal electron transport rate (ETRmax) in algae from deeper waters, are significantly reduced related to the original growth depth, while photosynthesis in the samples from 3 m water depth remains unaffected (Bischof et al. 1998b; Fig. 8).

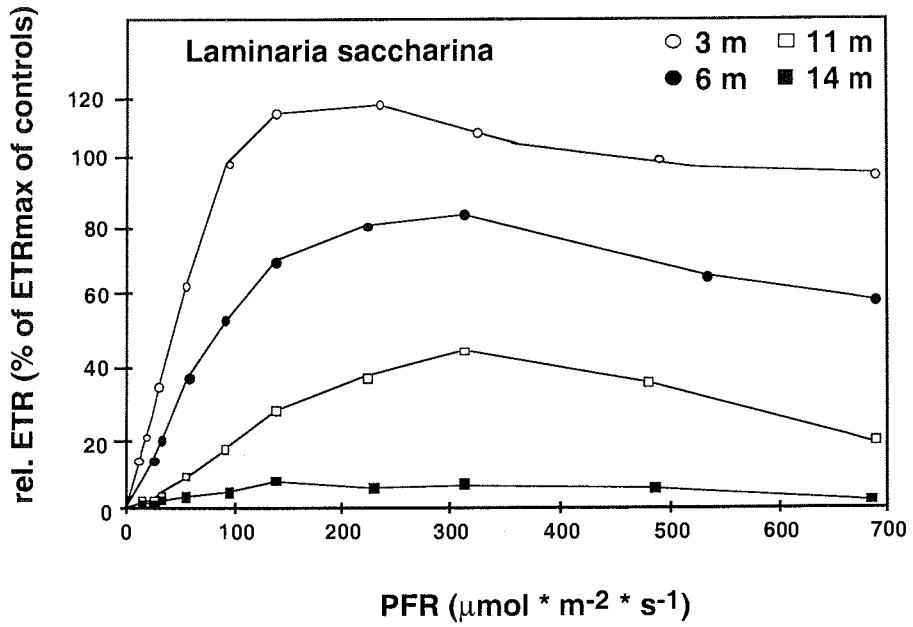

Fig. 8: Photosynthesis *vs.* irradiance curves as measured by a PAM-fluorometer on *Laminaria saccharina* collected from four different depths after 4 h of exposure to PAR + UVA + UVB. PFR = photon fluence rate of actinic white light; ETR = electron transport rate. Relative ETR is expressed as % of ETRmax values in controls, sampled from the respective water depth. Figure redrawn from Bischof et al. (1998b).

The respective contribution of each wavelength range (UVA + UVB, UVA and UVB separately) to the overall inhibitory effect of experimental irradiances was also analysed. UVA is adversely affecting maximal electron transport rates in the samples from 11 and 14 m depth. Additional effects of UVB are small in samples from 6 and 11 m, but the samples collected at 14 m depth are strongly affected by UVB (Bischof et al. 1998b; Fig. 9). Also, apart from the degree of inhibition of photosynthesis, there are marked differences in the rate of recovery from inhibition in samples from different depths: specimens from shallow waters show a significantly faster recovery (Bischof et al. 1998b)

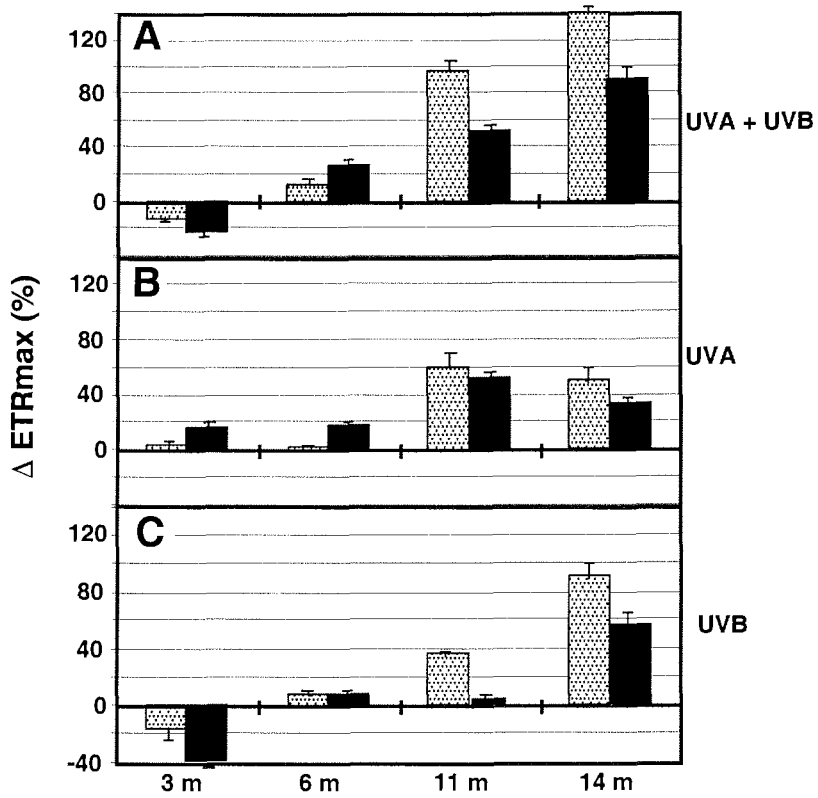

Fig. 9: Contribution of different wavelength ranges to the overall inhibition of maximal photosynthetic electron transport in *L. saccharina* expressed as the difference in ETRmax values (% of control values) measured under PAR and PAR + UVA + UVB (A), PAR and PAR + UVA (B), and PAR + UVA and PAR + UVA + UVB (C). Dotted bars: after 4 h of exposure; black bars: after 24 h of recovery. Figure redrawn from Bischof et al. (1998b).

Similar responses as for *L. saccharina* are also exhibited by the brown algae *Alaria esculenta* and *Saccorhiza dermatodea* (Bischof et al. 1998b). The results show that brown algae do acclimate to the radiation conditions (including UVB) at the different growth sites, allowing them to establish over a wide range of different water depths. Two physiological strategies are involved in acclimation: the reduction of the degree of inhibition, and the increase of the recovery rate.

The time course for acclimation of maximal quantum yield of photosynthesis was studied in more detail in the Arctic/cold-temperate brown alga *Alaria esculenta* (Bischof et al. 1999). This alga adjusts the maximal quantum yield of photosynthesis to changing radiation conditions within very few days. Specimens were collected under the ice, where algae were subjected to darkness or only low light without UVR for more than 6 months during the Arctic winter. Samples were then exposed to several repeated exposure cycles of various conditions of UVR and PAR irradiances. After each exposure, samples were transferred for 44 h to dim light conditions to permit recovery. Maximal quantum yields in algae collected under the ice decrease strongly and recover slowly when samples are exposed to UVR accompanied by low irradiances of PAR for the first time. During the second and third exposure cycle, Fv/Fm decreases to a similar extent but recovery proceeds significantly faster. During the following exposure cycles the degree of inhibition of maximal quantum yield decreases (Bischof et al. 1999; Fig. 10). However, the reduced sensitivity to UVR, which is achieved within a few days, is rapidly lost again after some days in dim light under UVR exclusion (Bischof et al. 1999).

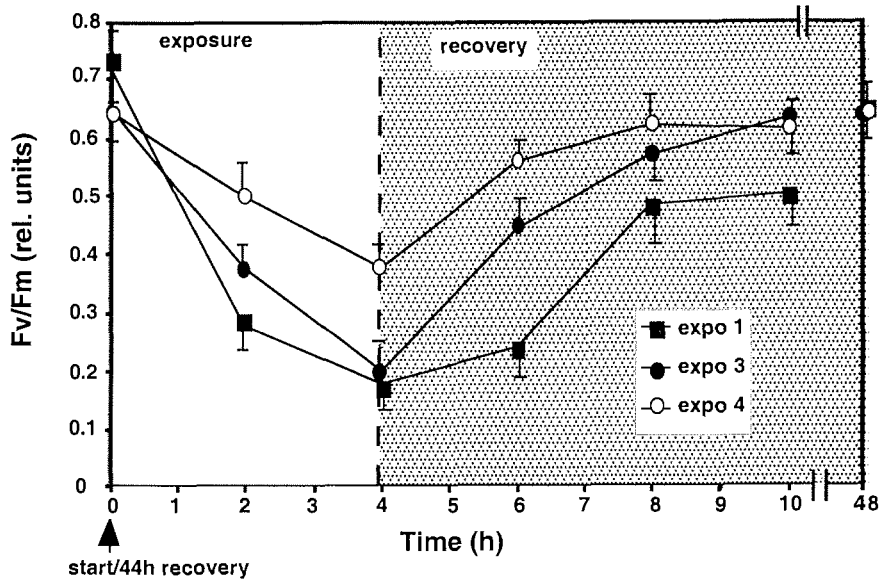

Fig. 10: Changes in maximal quantum yield of photosynthesis (Fv/Fm) in the Arctic/cold-temperate brown alga *Alaria esculenta*, collected under the sea-ice and exposed to repeated exposure cycles of 60 µmol m^{-2} s^{-1} PAR, 8 W m^{-2} UVA and 0.8 W m^{-2} UVB, for 4 h and subsequent recovery in dim light for 44 h, for the 1st, 3rd and 4th exposure cycle. Figure changed after Bischof et al. (1999).

A similar pattern of acclimation is observed when low light acclimated samples are exposed to repeated exposure cycles of high PAR (Bischof et al. 1999). Exposing high light acclimated algae to high levels of PAR plus UVB does not result in an enhanced inhibition of maximal quantum yield but in a delay of recovery (Bischof et al. 1999). On the other hand, when high light acclimated algae are exposed to UVB combined with low irradiance of PAR, only a very weak inhibition is observed (Bischof et al. 1999; Fig. 11).

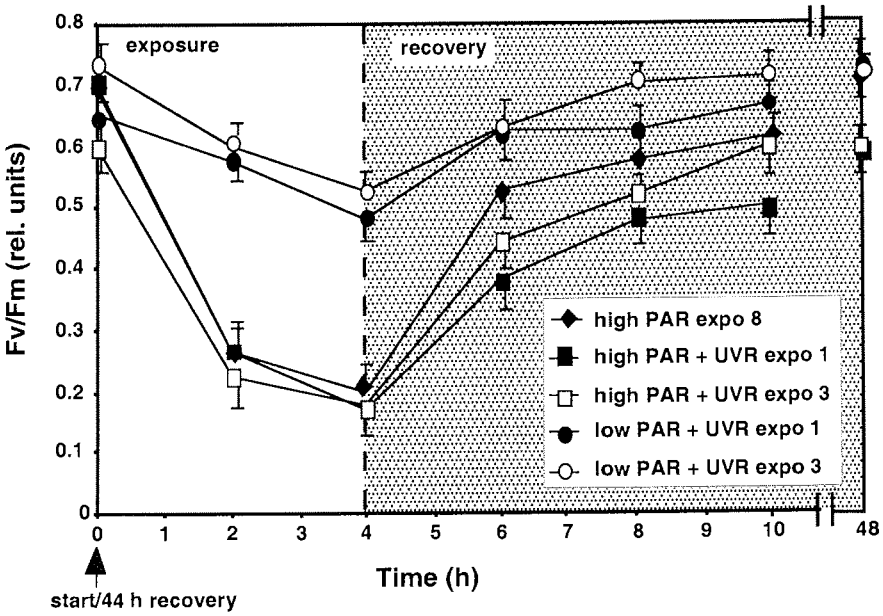

Fig. 11: Changes in maximal quantum yield of photosynthesis (Fv/Fm) in the Arctic/cold-temperate brown alga *Alaria esculenta*, collected under the sea-ice and exposed to repeated exposure cycles of 800 µmol m^{-2} s^{-1} PAR for 8 times (high PAR), and subsequently exposed to repeated exposure cycles of 800 µmol m^{-2} s^{-1} PAR, 8 W m^{-2} UVA and 0.8 W m^{-2} UVB (high PAR + UVR) or 60 µmol m^{-2} s^{-1} PAR, 8 W m^{-2} UVA and 0.8 W m^{-2} UVB (low PAR + UVR), for 4 h and subsequent recovery in dim light for 44 h. Figure changed after Bischof et al. (1999).

This demonstrates the synergistic effects of UVR and PAR in the field. At the natural growth site, photoinhibition seems to be predominantly caused by white light, whilst UVR results in a delay of the recovery process. Similar results were obtained from specimens, which were grown in the laboratory where they were previously cultivated under low light conditions without UVR and exposed to repeated exposure cycles of PAR and UVR (Bischof et al. 1999).

3.2.2. *UVR effects on photosynthesis - field experiments*

In turbid waters, UVR is strongly absorbed within the water column, and therefore is hardly affecting photosynthesis of sublittoral species at their natural growth site (Brouwer et al. 2000). *In situ* experiments on *Laminaria saccharina* were conducted in the Kongsfjord by using UVR transparent, submersible incubation chambers, wrapped with different cut-off foils. No significant differences in maximal quantum yield are found between samples exposed at 2 m depth under white light only compared to the samples receiving the full wavelength range of natural solar radiation (Brouwer et al. 2000). From the experimental set-up at 2 m water depth, part of the samples were harvested, transferred to the laboratory and exposed to extra UVB. There, samples previously cultivated under UVB exclusion respond with a reduction of Fv/Fm to about 20% of controls, while samples grown under the PAR+UVA+UVB treatment are lesser, although still strongly, affected. After UVB exposure has ceased, all samples recover rapidly and completely. In the outdoor set-up, solar irradiance was increased by moving the incubation chambers, including the algae, from 2 m to 1 m water depth. After 5 days of incubation under these conditions, maximal quantum yield in samples receiving UVR is strongly decreased compared to the samples which were shielded from solar UVR (Brouwer et al. 2000). However, the additional UVR exposure in the laboratory results in a significantly smaller reduction in Fv/Fm than before, but nevertheless the samples previously cultivated under PAR only, are slightly more strongly inhibited. After the algae were kept at 1 m water depth for two weeks, samples have acclimated to the new radiation conditions at 1 m water depth, as no differences in maximal quantum yield between samples from different radiation treatments are found (Brouwer et al. 2000). Moreover, the subsequent UVR exposure in the laboratory does not result in any reduction of Fv/Fm in samples previously receiving the full solar spectrum within the incubation chambers. However, samples kept under UVB exclusion exhibit a strong reduction of Fv/Fm during exposure to extra UVB. The red alga *Palmaria palmata* was tested in the same way: in accordance with its higher occurrence on the shore, this species is more tolerant to UVR exposure than *L. saccharina*,

as indicated by the smaller reduction of maximal quantum yield in samples harvested from 2 m water depth and exposed to extra UVB (Brouwer et al. 2000).

In another field study conducted at the Kongsfjord, experimental specimens of six macroalgal species underwent a transplantation experiment, and the changes of maximal quantum yield of photosynthesis in relation to the changed radiation conditions have been studied (Karsten et al. 2000). Samples of two brown algal species (*Laminaria solidungula, Saccorhiza dermatodea*) and four red algal species (*Palmaria palmata, Phycodrys rubens, Phyllophora truncata, Ptilota plumosa*) were collected from deeper waters, transplanted to 1, 3 and 4-5 m water depth and covered with different filter foils, cutting off different spectral ranges. In regular intervals, maximal quantum yield of photosynthesis was determined. Results obtained support the vertical zonation pattern of the individual species on the shore, i.e. Fv/Fm values in shallow-water species like *P. palmata* change least (Karsten et al. 2000), while deep-water species such as *P. rubens* respond very sensitively to the radiation conditions in shallow waters (Karsten et al. 2000). In the deep-water species, the impinging UVB contributes significantly to the overall inhibition of photosynthesis (Karsten et al. 2000). In all species but *P. truncata*, adverse effects of UVB are absent in samples incubated at 3 m water depth or deeper. The results indicate the differential ability of species to cope with enhanced radiation, which might be partly based on differential genetic preconditions.

3.2.3. *Effects on brown algal zoospores*

A different degree of acclimation to UVR is also reflected by the sensitivity of brown algal zoospores. Photosynthesis, germination capacity and DNA damage were studied in brown algal zoospores from Spitsbergen and Southern Spain during a 16 h exposure to artificial UVR (Wiencke et al. 2000). Generally, the germination capacity of spores from species collected in greater water depth is more strongly impaired after exposure to the same UVR doses

than species from shallow waters, with the UVB range being the most effective (Wiencke et al. 2000; Fig. 12).

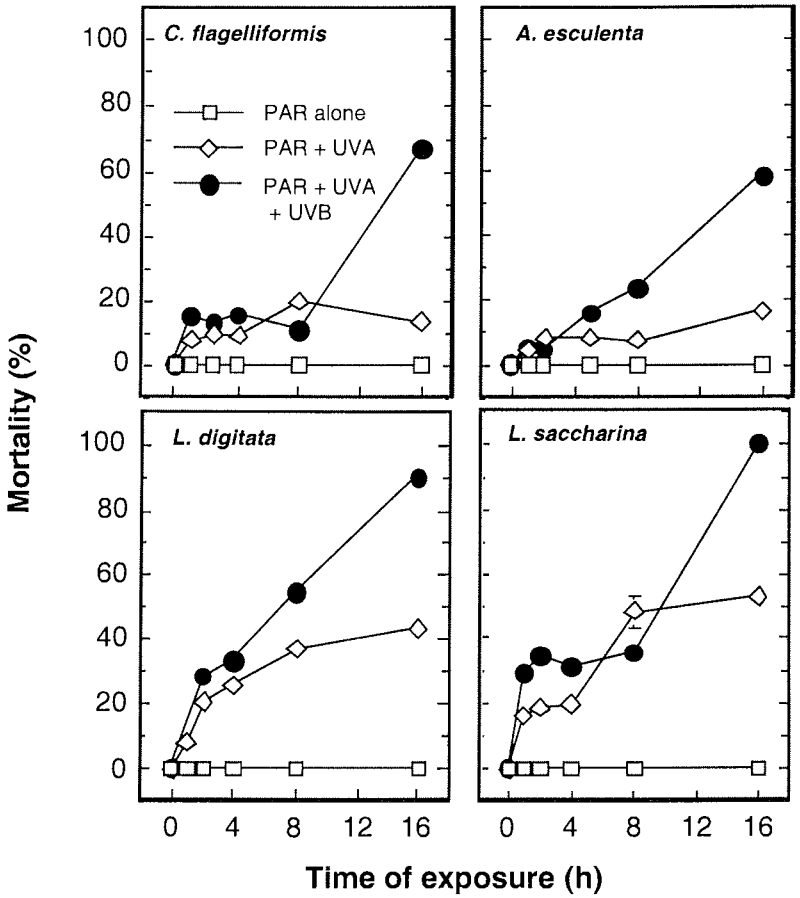

Fig. 12: Mortality of zoospores from brown algal species from the upper (*Chordaria flagelliformis, Alaria esculenta*) and the middle sublittoral *zone (Laminaria digitata, Laminaria saccharina*) from Spitsbergen during 16 h of exposure to 6.5 W m^{-2} PAR, 7.6 W m^{-2} UVA and 0.6 W m^{-2} UVB. Figure changed after Wiencke et al. (2000).

Within the Arctic species, viability of zoospores of *Laminaria digitata* and *L. saccharina* is very strongly impaired by UVB radiation, with up to 100% dead spores by the end of exposure. Spores of *Alaria esculenta* and *Chordaria flagelliformis* exhibit a mortality rate of 60% under the UVB treatment, while mortality of spores under UVB exclusion is low (20%). In order to cause 50% spore mortality in the two latter species, spores need to be exposed to more

than the double of the weighted UVB dose required for the same degree of mortality in the *Laminaria*-species (Wiencke et al. 2000).

For *Laminaria digitata*, loss of zoospore viability is shown to be a result of DNA damage due to thymine dimer formation, which linearly increases as a function of the increasing UVB dose (Wiencke et al. 2000; Fig. 13).

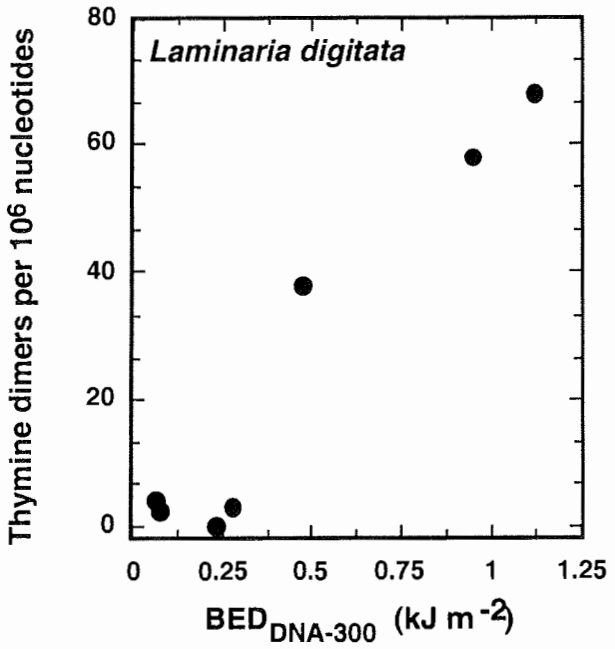

Fig. 13: Relationship between the DNA damage measured as thymine dimer formation in *Laminaria digitata* and the biologically effective dose (BED) of irradiances weighted using the action spectra for DNA damage described by Setlow (1974). Figure redrawn from Wiencke et al. (2000).

Moreover, in contrast to the large sporophytes, UVB exposure of spores results in a strong impairment of the photosynthetic apparatus, as measured by chlorophyll fluorescence (Wiencke et al. 2000). Zoospores from brown algae collected in Southern Spain are particularly sensitive to UVB exposure, with the deep-water *Phyllariopsis*-species being the most sensitive and *Saccorhiza polyschides* from shallower waters being the most tolerant species (Wiencke et al. 2000).

In summary, spores appear to be the life history stage most strongly sensitive to UVR, and therefore, they are of prime importance for the determination of the upper depth zonation limit of brown algae. This is particularly exhibited in the brown algal species from Southern Spain: germination of spores of the Laminarian species examined from this region is prevented by exposure to UVB irradiances occurring at water depths lower than 7 m (Wiencke et al. 2000), which is in accordance with the vertical zonation pattern in the field.

3.3. Protection against UVR

An important step in acclimation to changing irradiance may include the shielding of critical cellular components from harmful radiation. This can be achieved by the synthesis of UVR screening compounds. The induction of the synthesis of UVR absorbing MAAs was studied in the Arctic endemic red alga *Devaleraea ramentacea* (Karsten et al. 1999). Seven different MAAs are detected in this species, namely mycosporine-glycine, shinorine, porphyra-334, palythine, asterina-330, palythinol, and palythene. Particularly the UVB component of the natural solar spectrum is very effective in inducing the formation of MAAs in this species, as shown under filtered solar radiation in the field. After transplantation of samples from 2 m water depth to the surface and exposure under various radiation conditions for one week, the total MAA content in samples exposed to the whole range of natural solar radiation has almost doubled in comparison to the initial values. This increase in total MAA content is predominantly due to the formation of palythine. Algae exposed only to PAR or PAR + UVA do not show significant differences in total MAA content (Karsten et al. 1999; Fig. 14).

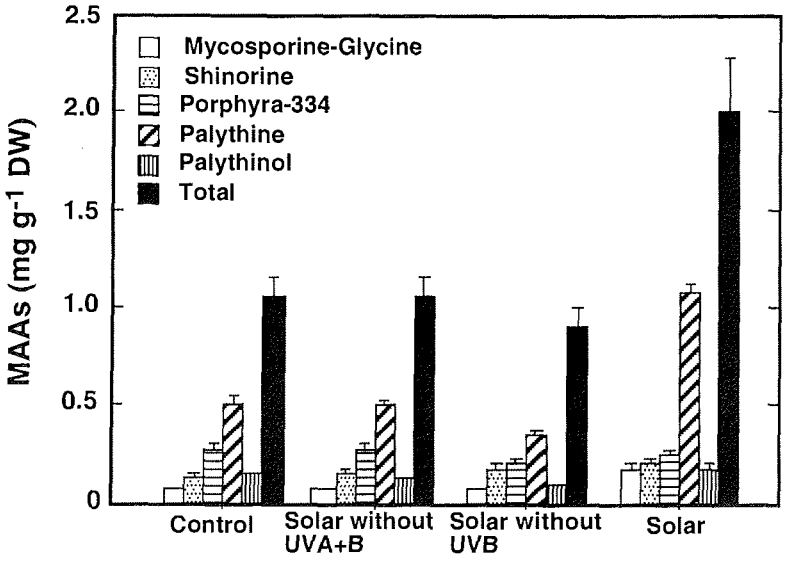

Fig. 14: *Induction of the synthesis of mycosporine-like amino acids (MAAs) in the Arctic endemic red alga Devaleraea ramentacea from Spitsbergen, one week after specimens were transplanted from 2 m water depth to the surface, where they were exposed to various solar radiation treatments; control = MAA content in samples collected at 2 m water depth. Figure redrawn from Karsten et al. (1999).*

Also, specimens sampled from sun exposed locations contain approximately two times higher amounts of total MAAs than samples collected from the understorey on the same day from the same water depth. Again, the higher amount of MAAs in algae from sun exposed locations is predominantly due to the high concentration of palythine which is almost three times higher than in the understorey algae (Karsten et al. 1999). Specimens exposed to high solar radiation in the field generally exhibit green apices and a red coloured base. Total MAA content in the apices is up to 5 fold higher than in the base, also Chl *a* concentration is 5 fold higher in the tips. In contrast, the phycobiliproteins phycoerythrin and phycocyanin can only be detected within the red basal tissue (Karsten et al. 1999). A gradual decrease in total MAA content is found with increasing collecting depth of samples. Moreover, there is a marked seasonal effect. Samples collected in June contain significantly lower MAA concentrations as compared with specimens sampled from the same locations in August at the end of the Arctic summer (Karsten et al. 1999; Fig. 15).

Maximal electron transport rates after exposure of *D. ramentacea* to artificial UVR are reduced according to the respective collection depth of samples, and, in turn, in relation to decreasing MAA content (Karsten et al. 1999). The strong correlation between MAA content and the degree of inhibition of photosynthetic electron transport after exposure to artificial UVR shows the potential of MAAs to partly protect photosynthesis against harmful radiation (Karsten et al. 1999).

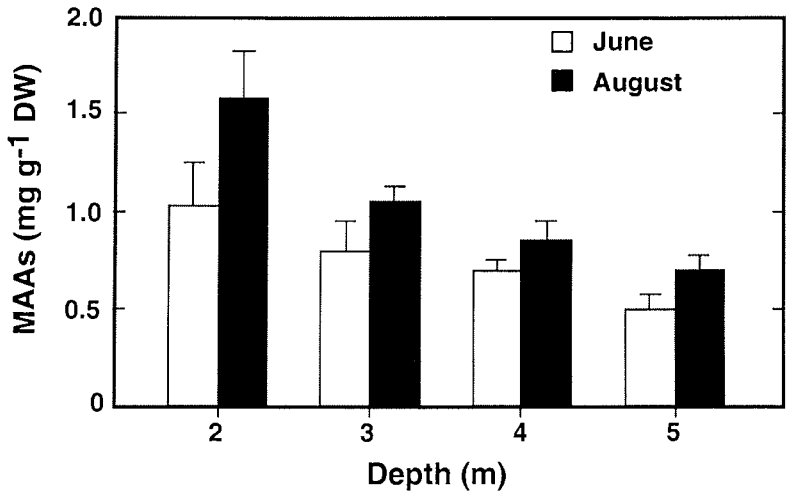

Fig. 15: Changes in MAA content in *Devaleraea ramentacea* in relation to collection depth and season. Figure redrawn from Karsten et al. (1999).

The differences in the content and composition of MAAs as a possible factor involved in the vertical distribution of red macroalgal species was studied in *Mastocarpus stellatus* and *Chondrus crispus* from Helgoland (Bischof et al. 2000b). Specimens were sampled from populations at the same shore level and subsequently exposed to artificial UVR. The effects measured are almost exclusively due to the exposure to UVB, while UVA induces only very small effects on the parameters tested. Photosynthetic characteristics, such as effective ($\Delta F/Fm'$) and maximal quantum yield (Fv/Fm) as well as maximal electron transport rate (ETRmax), are more strongly inhibited due to UVB exposure in *C. crispus* than in *M. stellatus* (Bischof et al. 2000b; Fig. 16).

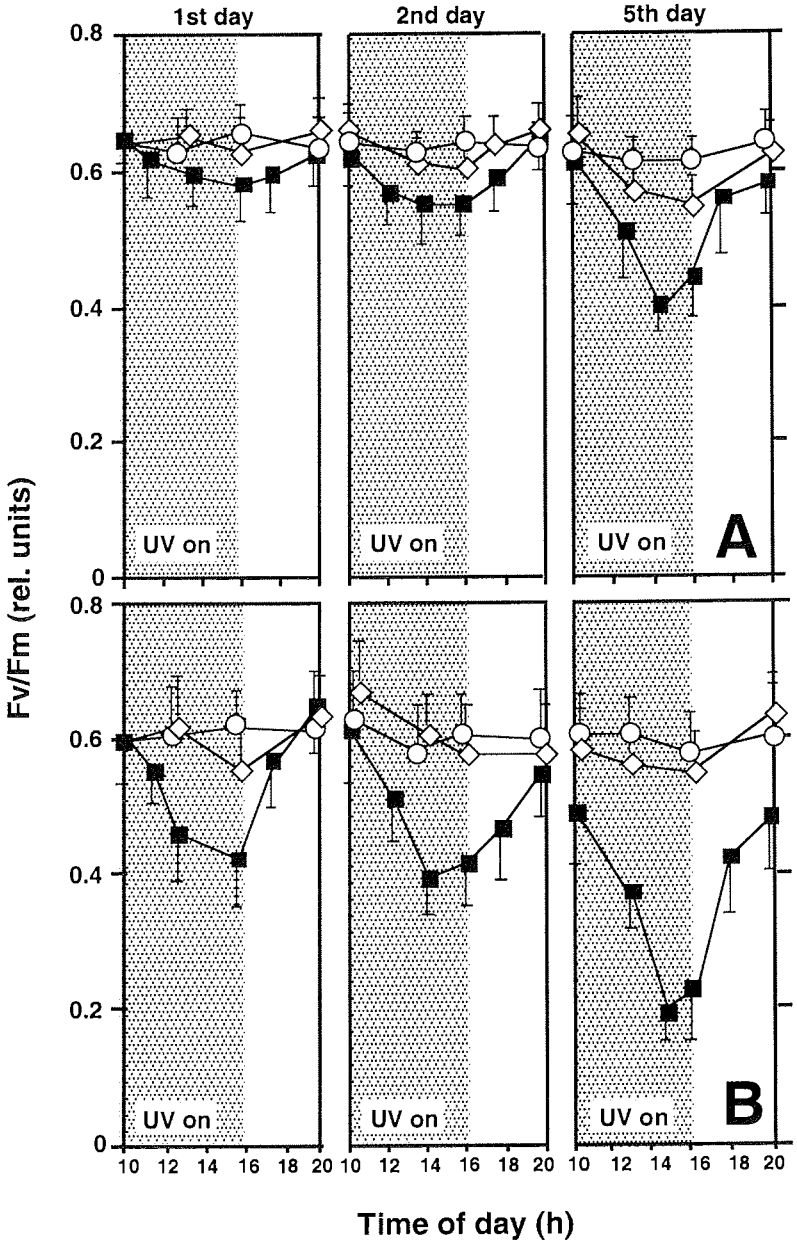

Fig. 16: Maximal quantum yield of photosynthesis (Fv/Fm) in *Mastocarpus stellatus* (A) and *Chondrus crispus* (B) during exposure (dotted area) to PAR (○), PAR + UVA (◇), and PAR + UVA + UVB (■) and subsequent recovery in PAR only, for the 1st, 2nd and 5th day of treatment. Figure redrawn from Bischof et al. (2000b).

These results are in accordance with the observation that *M. stellatus* occupies generally a higher position on the shore. Adverse effects of UVB on total activity of RubisCO are not exhibited by the two species under the respective experimental conditions (Bischof et al. 2000b).

The differences in resistance of photosynthesis to UVR may result from the respective composition of UVR screening MAAs, which is markedly different in the two species (Bischof et al. 2000b; Table 1). Samples of *C. crispus* contain 0.430 mg of total MAAs per g dry weight before the start of exposure. MAAs detected in initial samples are namely palythine, asterina, and palythene; at that time no shinorine was found. By the end of the experiment, total MAA content has increased by 55%. While the concentration of palythine remains unchanged, the levels of asterina and palythene almost doubles. Moreover the *de novo*-synthesis of shinorine strongly contributes to the increase in total MAA content. In contrast, shinorine is the only MAA which can be detected in *M. stellatus*. However, its initial concentration is 6 times higher than total MAA concentration in *C. crispus* at the start of the experiment. After five days, internal MAA concentration (still only shinorine) in *M. stellatus* has increased by 100% (Bischof et al. 2000b). The concentration of screening compounds, which contribute to the different sensitivities to UVR, may be an additional factor determining the depth zonation of the species.

Table 1 Composition and content of mycosporine-like amino acids in *Chondrus crispus* and *Mastocarpus stellatus*, in samples taken before the start of the experiment and after the end of the fifth exposure to UVB, mean values (n=3) ± SD. Data taken from Bischof et al. (2000b).

Compound	Absorption maximum (nm)	*C. crispus* Initial content	(mg*g DW^{-1}) Final content	*M. stellatus* Initial content	(mg*g DW^{-1}) Final content
Shinorine	334	no trace	0.118 (±0.025)	2.650 (±0.500)	4.440 (±1.090)
Palythine	320	0.294 (±0.087)	0.285 (±0.107)	no trace	no trace
Asterina	330	0.089 (±0.023)	0.167 (±0.079)	no trace	no trace
Palythene	360	0.042 (±0.003)	0.092 (±0.019)	no trace	no trace
Σ MAAs		**0.430 (±0.113)**	**0.670 (±0.221)**	**2.650 (±0.500)**	**4.440 (±1.090)**

3.4. UVR effects on photosynthetic dark reactions

In a biochemical approach, the UVR effects on the photosynthetic pathways were studied on cultivated algal material (Bischof et al. 2000a). Five macroalgal species (*Monostroma arcticum, Palmaria palmata, Alaria esculenta, Laminaria solidungula, Phycodrys rubens*), originally isolated at the Kongsfjord (Spitsbergen), were exposed to artificial UVR for up to 72 h. Studied parameters included: maximal quantum yield (Fv/Fm) and maximal electron transport rate (ETRmax) of photosynthesis, content of Chl *a* and proteins, activity of the two Calvin cycle enzymes ribulose-1,5-bisphosphate carboxylase/oxygenase (RubisCO) and glyceraldehyde-3-phosphate dehydrogenase (G3PDH), and content of RubisCO. In all species studied, Chl *a* content, maximal quantum yield and maximal electron transport rate decrease during UVR exposure. Decreasing photosynthetic rates are partly due to decrease in RubisCO activity. The observed reduction in the total activity of RubisCO may either be due to its deactivation *per se* or due to the degradation of the enzyme.

M. arcticum is the least sensitive species, exhibiting the smallest reduction of ETRmax during exposure (Bischof et al. 2000a; Fig. 17). RubisCO activity remains unaffected during the first 36 h. Subsequently, the activity drops down to 53% of its activity before exposure.

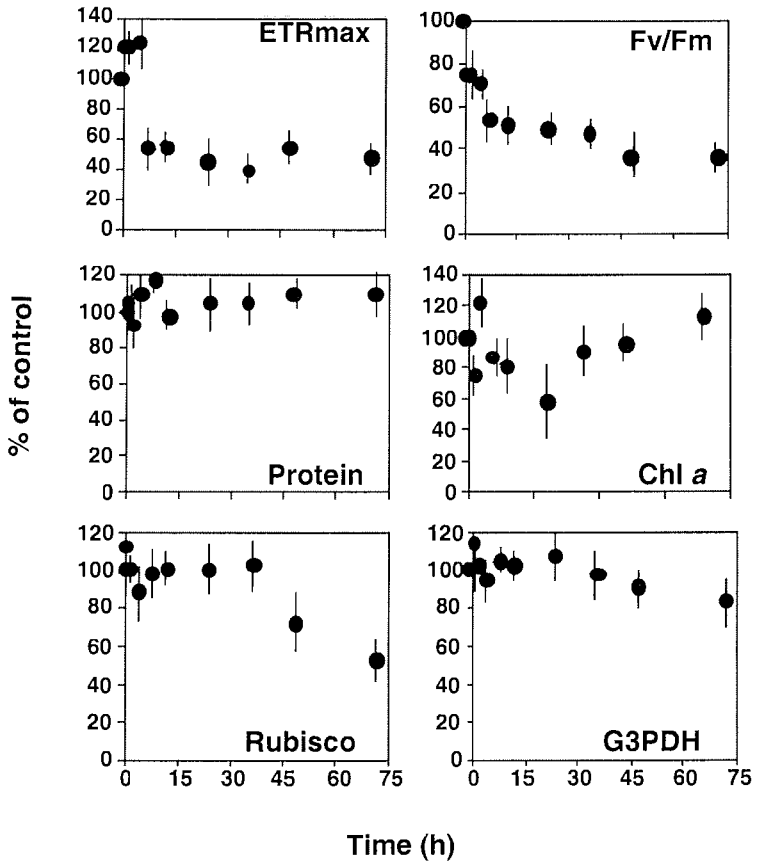

Fig. 17: Changes in maximal photosynthetic electron transport rate (ETRmax), maximal quantum yield of photosynthesis (Fv/Fm), content of protein (Protein) and chlorophyll a (Chl a), activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and glyceraldehyde-3-phosphate dehydrogenase (G3PDH) during exposure of *Monostroma arcticum* to UVR. Figure redrawn from Bischof et al. (2000a).

In *M. arcticum*, declining activity may be attributed to the UVR induced loss of the large and small subunits of RubisCO as it is documented by SDS-PAGE (Bischof et al. 2000a; Fig. 18).

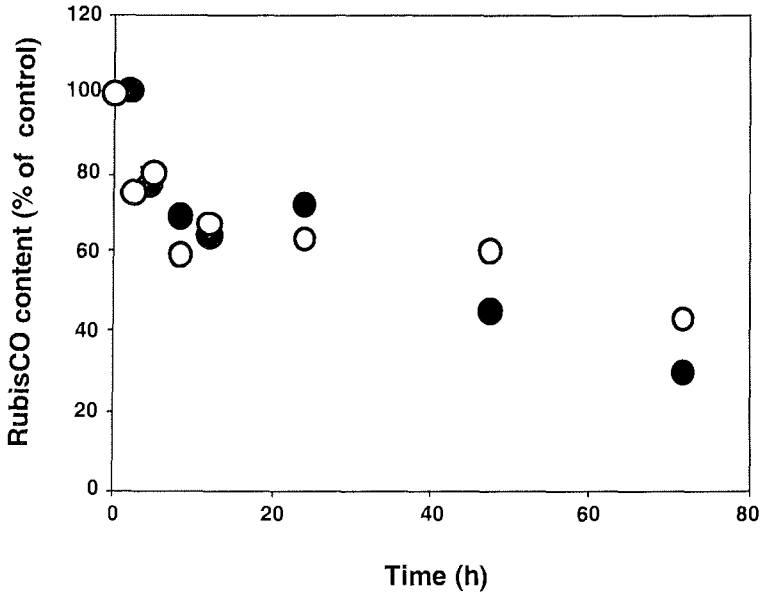

Fig. 18: Changes in RubisCO subunit content during UVR exposure of *Monostroma arcticum*, as studied by densitometry of SDS gels; (●) large subunit, (○) small subunit. Figure redrawn from Bischof et al. (2000).

In *A. esculenta*, Fv/Fm values as well as ETRmax and RubisCO activity decline rapidly. A reduction in the amount of the large and small subunits of RubisCO is demonstrated clearly by SDS-PAGE. In parallel with this decline, a band with a higher molecular weight becomes more prominent in the gel, indicating the UVR induced aggregation of non-functioning protein generated from degraded RubisCO subunits (Bischof et al. 2000a; Fig. 19). In contrast to the high sensitivity of RubisCO, in all species tested, G3PDH is much more resistant to UVR (Bischof et al. 2000a).

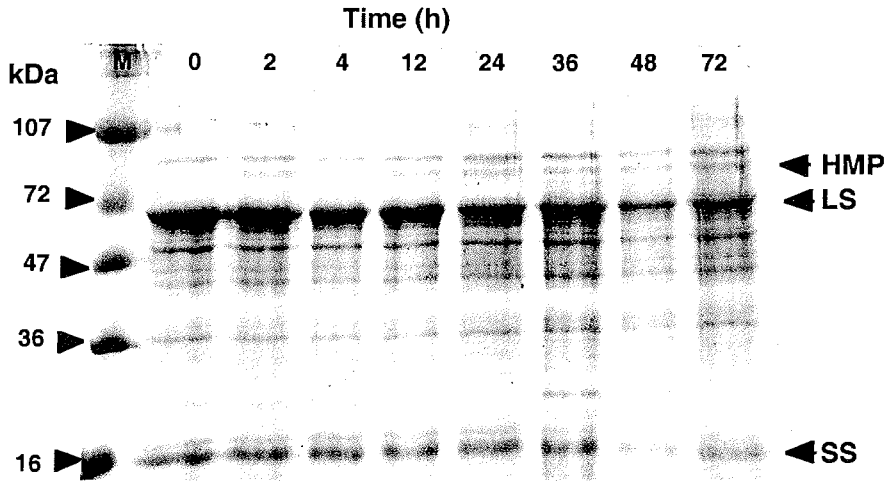

Fig. 19: SDS gel on crude extracts of *Alaria esculenta* after 0, 2, 4, 12, 24, 36, 48 and 72 h of UVR exposure. M = molecular weight marker (kDa = kilodalton), HMP = high molecular weight polypeptide, LS and SS = large and small subunit of RubisCO, respectively. Figure redrawn from Bischof et al. (2000a).

Typical algae from the lower sublittoral zone as *Laminaria solidungula* and *Phycodrys rubens* are very sensitive to prolonged artificial UVR exposure for all parameters tested; a strong and rapid decline of the fluorescence and biochemical parameters is exhibited by these species. In contrast to the other species studied, a marked loss of total proteins, probably due to cell leakage, is also documented (Bischof et al. 2000a; Fig. 20).

Again, this different approach using biochemical parameters support the finding that the sensitivity to UVR is related to the depth distribution of these species in the field.

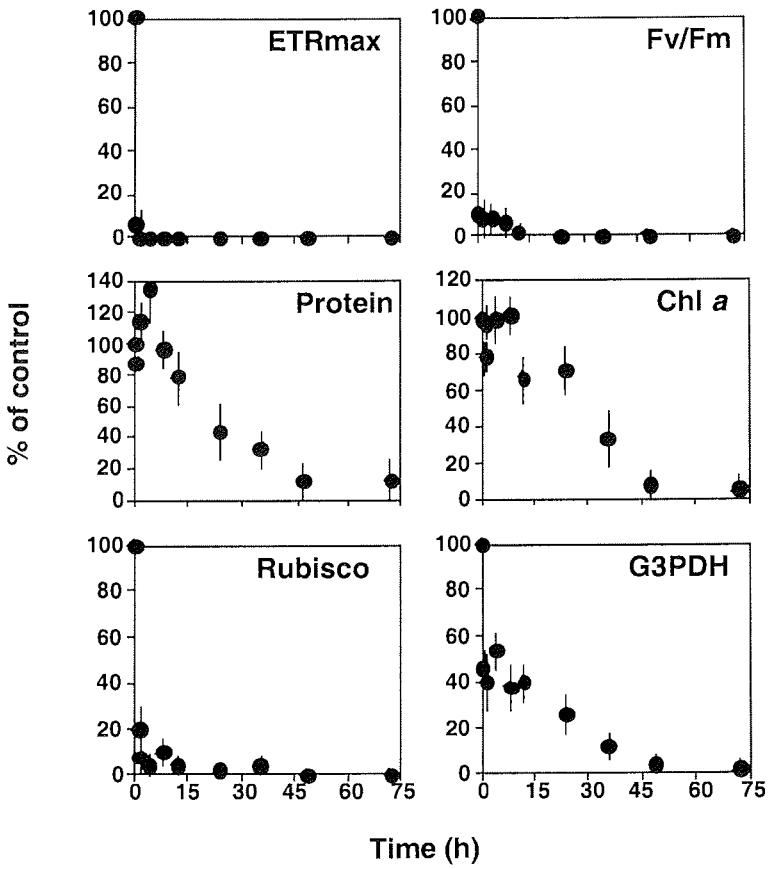

Fig 20: Changes in photosynthetic and biochemical parameters during UVR exposure of *Phycodrys rubens*; details as in Fig. 17. Figure redrawn from Bischof et al. (2000a).

4. DISCUSSION

4.1. Methodological considerations

4.1.1. *PAM fluorescence measurements*

Throughout this study, one of the important measurements was to determine variable chlorophyll fluorescence of PS II to estimate photosynthetic performance. Recently this technique has become established in modern photosynthesis research. An overview on the basics and applications are given by Krause and Weis (1991) and Schreiber et al. (1994). Further improvements of available devices include a higher resolution of the measuring signal and more comfortable handling, thus, allowing the use of portable fluorometers in field studies. Meanwhile, a large number of field studies have been conducted on macroalgae and seagrasses by means of portable devices (e.g. Hanelt 1992; Larkum and Wood 1993; Hanelt and Nultsch 1995; Dawson and Dennison 1996; Häder et al. 1996; Hanelt et al. 1997a; Sagert et al. 1997; Gómez and Figueroa 1998; Gómez et al. 1998). Measuring PAM fluorescence offers two advantages compared to commonly used techniques of oxygen evolution or CO_2 fixation measurements: (1) PAM fluorescence is a non-invasive method, therefore measurements can be conducted without stressing or damaging the plant (Bilger et al. 1995), and (2) it allows a fast assessment of photosynthetic activity. Consequently, a much higher number of samples can be measured in the course of an experiment.

The maximal quantum yield of photochemistry is a commonly used parameter in stress research and expressed as the ratio of variable to maximal chlorophyll fluorescence (Fv/Fm). It indicates the efficiency of energy transfer from the antennae systems to the reaction centres. Until now, there are several studies on macroalgae showing, with a few exceptions (e.g. Hanelt and Nultsch 1995), the good agreement of photoinhibition experiments as performed by measuring oxygen evolution and changes in Fv/Fm. Hanelt et al. (1992) demonstrated a linear relationship between Fv/Fm and gross-oxygen evolution during photoinhibition. These results are in line with a study on UVR effects on

photosynthesis of different developmental stages of *Laminaria* species from Helgoland, where a significant positive correlation between oxygen evolution and Fv/Fm was found (Dring et al. 1996a).

Considering Fv/Fm measurements in algae, it must be noted that the PAM technique was originally developed for higher plants with a different pigment composition, and thus, different fluorescence emission of the photosynthetic apparatus (Büchel and Wilhelm 1993). To guarantee the reliability of PAM measurements in the different algal groups this should be considered and the respective fluorescence parameters should be determined carefully. To determine Fo, the measuring beam must be strong enough to induce a high signal/noise ratio but must not induce charge separation. In particular, algal groups containing Chl *c* and phycobilins are able to photosynthesise under very low light intensities compared to green algae (Büchel and Wilhelm 1993). In order to determine Fm correctly, the saturating pulses must be strong enough to completely reduce the primary acceptors without inducing quenching mechanisms by energising the thylakoid membrane. Especially in red algae, a fast quenching of Fm appears to be likely (Hanelt 1996). Due to technical restrictions of the measuring device the maximal possible Fv/Fm ratios differ in the various algal groups. In Chlorophyta, Fv/Fm values up to 0.83 can be achieved, while in Phaeophyta 0.7-0.8 and in the Rhodophyta 0.6-0.7 have been reported for unstressed plants (Büchel and Wilhelm 1993). These differences in fluorescence emission are related to the different architecture and composition of the photosynthetic apparatus. In general, Chl *c* or phycobilin containing algae possess different thylakoid membrane arrangements and do also differ from higher plants and green algae with respect to the light harvesting complex (LHC) and the interaction between the antennae and the reaction centers, resulting in different features of absorption, excited energy transfer and distribution of excitation energy between the two photosystems. Consequently, Chl *c* or phycobilin containing algae often show high Fo values in relation to Fm (in the red algae due to fluorescence contributions from phycobili pigments; Franklin and Forster 1997), leading to the decreased Fv/Fm ratios (Büchel and Wilhelm 1993). Also, chlororespiration may be a reason for lower Fv/Fm values (Büchel and Wilhelm

1993). Due to these differences in maximal Fv/Fm values under non stressing conditions, it makes sense to relate measurements to the 100% of initial values to facilitate comparisons of measurements conducted on species from different algal groups.

In contrast to Fv/Fm, the effective quantum yield (ΔF/Fm´) reflects actual light utilisation during illumination of samples. This ratio decreases in response to increasing irradiation, as demonstrated during daily cycles in the field (Hanelt et al. 1994; Franklin et al. 1996; Gómez et al. 1998; Jiménez et al. 1998; Flores-Moya et al. 1999). In Bischof et al. (2000b), ΔF/Fm´ was measured with a Diving-PAM (Walz, Germany) to test whether differences in light utilisation were present in the two species tested during UVR exposure. The high significance of these data derives from the fact that measurements of effective quantum yield were performed *in situ* (i.e. under the actual radiation conditions; c.f. Hanelt et al. 2000b). In order to obtain reliable results with this technique it has to be considered that changes in ambient radiation result in changes in ΔF/Fm´. This is especially valid when applying this technique to field measurements, where strong variations in irradiance are present within the same algal community (Hanelt et al. 2000b). Consequently, ΔF/Fm´ data may vary strongly between samples, therefore, an even irradiation in addition to a high number of replicates are necessary prerequisites for reliable data sets. The ecophysiological significance of ΔF/Fm´ measurements is high, as this parameter has been shown to be significantly correlated with the yield of CO_2 assimilation (Genty et al. 1989); ΔF/Fm´ represents the so called "Genty-parameter".

Photosynthesis *vs.* irradiance curves (PI-curves) were recorded with the PAM fluorometer to determine maximal electron transport rates (ETRmax), in order to estimate also photosynthetic capacity (Schreiber et al. 1994). Direct linear or curvilinear relationsships between photosynthetic rates as measured with oxygen electrodes and those measured as ETRs with a PAM fluorometer have been shown in studies on *Ulva*-species (Chlorophyta) and seagrasses (Beer et al. 1998b, 2000). Apart from the presented study, there are very few publications available containing PAM recorded PI-curves for photoinhibition studies on macroalgae (Bischof et al. 1998a; Flores-Moya et al. 1998; Gómez

and Figueroa 1998), although this provides useful additional information about different aspects involved in UVR induced photoinhibition. Moreover, PI-curves can be rapidly recorded with the fluorometer. Throughout our studies, complete curves were recorded within 5 minutes with an increase in actinic irradiance at every 30 seconds. While some authors do measure respective ETRs not until after several minutes of actinic irradiation (Schreiber et al. 1994), Beer et al. (1998b) have shown for 3 seagrass species that 30 to 40 seconds of irradiation at each light level are sufficient to reach optimal ETR values. This is in line with studies on photosynthetic activity of symbiotic zooxanthellae in corals (Beer et al. 1998a) as well as with our own preliminary studies on various macroalgal species, comparing ETR curves performed with different lengths of actinic irradiance. White and Critchley (1999) showed that even faster light curves with only 10 seconds at each irradiation step may provide reliable information on the state of the photosynthetic apparatus.

Measurements of Fv/Fm, $\Delta F/Fm'$ or ETRmax reflect the overall contribution of several physical and molecular processes to photosynthetic performance, but do not clearly provide evidence on the mechanisms behind these effects. Analysis of quenching parameters may provide additional information (Havaux et al. 1991), but were only performed once in this study to monitor changes in photochemical (qP) and non-photochemical quenching (qN) during the on- and off-set of UVR exposure (Bischof et al. 1999).

In conclusion, as shown in this thesis as well as in a continuously growing number of other publications, measuring PAM fluorescence represents a suitable technique for rapid assessment of stressful conditions to plant metabolism (Krause and Weis 1991; Schreiber et al. 1994) and it is also a simple means to detect UVR stress in algae (Clendennen et al. 1996; Cordi et al. 1997; Hanelt et al. 1997a). With a fast assessment of photosynthetic activity it is possible to study the response to solar radiation in algae from different treatments in parallel, and moreover, with a sufficiently high number of replicates. The latter is hardly possible with measurements of oxygen evolution. However, when relating the results of PAM measurements to the organismic level it should be kept in mind that fluorescence measurements only provide relative data, which is sufficient when performing comparative studies. As PAM

fluorometry measures only photon-driven electron transport (which gives rise to oxygen evolution, but also to photorespiration), it cannot be applied by itself if energy or gas exchange are to be determined, since these depend on the diurnal rates of dark respiration (Beer et al. 1998b). Therefore, in order to estimate changes in e.g. primary production, fluorescence data still have to be correlated with measurements of CO_2 fixation or oxygen evolution and growth. It is also obvious that UVR exposure may exert effects on plant life (changes in growth rate, reproductive success) which are not necessarily reflected neither by changes in the fluorescence signal nor in measurements of photosynthesis at all. Even if fluorescence data indicate acclimation to experimental conditions, this does not necessarily imply that the experimental individuals are unaffected. Therefore, future studies should monitor additional parameters of UVB induced impairment of plant metabolism (Cordi et al. 1997; van de Poll unpublished).

4.1.2. *Photometric RubisCO assays*

To estimate changes in RubisCO activity under UVR exposure, a photometric test was used as described by Gerard and Driscoll (1996). Despite the high significance of data on UVR induced impairment of RubisCO activity, some limitations of the used technique have to be taken into account. The test is well suited for comparative studies by relating measured activities under UVR exposure to the 100% level of the initial values to compare the differences in sensitivity of RubisCO in the different species. Using not standardised values, absolute values of CO_2 fixation can be estimated assuming that two $NADH_2$ are oxidised per one CO_2 fixed (Gerard and Driscoll 1996). But the use of these absolute values results in a high variation of the data. Therefore, it is better to use this test only for relative measurements. It should also be noted that this test is only suitable for measurements of activity of the fully activated enzyme *in vitro*. No estimates of the *in vivo* activation state (the ratio of initial activity in the cell to the activity of the fully activated enzyme) can be made with this technique, which limits slightly the significance of the test. It was shown by Strid et al. (1990) that UVR exposure changes both initial activation and total activity

of RubisCO. However, despite these restrictions, the used technique was shown to be very helpful to document impairment of Calvin cycle enzymes.

4.1.3. *Experimental radiation conditions*

A critical point in most UVR studies conducted in the laboratory is the artificial UVR spectrum and exposure. The light sources used in laboratory experiments can hardly meet the natural spectrum in the field (Fig. 2). Experimental treatments with the widely used Q-Panel UVA-340 tube result in a UVB:UVA ratio of 1:10; the emission spectrum of the tubes is provided by Bischof et al. (1998a). From field measurements in the Arctic it is known that this ratio is rather 1:20 (Bischof et al. 1998b), and it is self evident that in the field, high UVR levels are always accompanied by high levels of PAR, which is hardly the case in laboratory treatments but most important for realistic ecological plant experiments (Teramura 1986; Döhring et al. 1996; Thiel et al. 1996). On a physiological basis, studies with a higher UVR to PAR ratio are of particular interest in revealing the mechanisms of UVR induced damage. However, a low PAR background avoids possible masking of UVR effects by excessive PAR (Molina and Montecino 1996; Nilawati et al. 1997). The low level of PAR used in most of the experiments was not regarded to be a limiting factor for physiological requirements as macroalgae from the Arctic in general are shade adapted species (Kirst and Wiencke 1995). Synergistic effects of PAR and UVR have to be considered when applying data from laboratory experiments to field conditions. There, UVR is particularly affecting the recovery from photoinhibition. Beside the UVR-induced delay in the recovery process in Arctic species (Hanelt et al. 1997a; Bischof et al. 1999, 2000c), the UVB range, in contrast to UVA, was also shown to promote recovery in the brown alga *Dictyota dichotoma* from Southern Spain and in a couple of freshwater macrophytes, as tested in New Zealand (Flores-Moya et al. 1999; D. Hanelt, Alfred Wegener Institute, pers. communication).

Also, cultivation conditions of samples prior to the experiments are of significant importance for the conclusions to be drawn in an ecological context.

It has been shown in studies on higher plants that the level of PAR during the cultivation of experimental plant material is very important for the sensitivity of samples to UVR during the experiment (Teramura 1986; Cen and Bornman 1990).

While being aware of these restrictions, laboratory experiments are very helpful tools to study specific mechanisms involved in UVR stress and allow the studies of differential genetically determined UVR sensitivity and ability to cope with UVR within the different species.

4.2. General discussion

4.2.1. *Impairment of photosynthesis*

Throughout the experiments conducted, a detrimental effect of UVR on photosynthesis of Arctic macroalgae was observed. Several previous studies demonstrate the impairment of macroalgal photosynthesis due to UVR exposure in the laboratory (Dring et al. 1996a, b; Bischof et al. 1998a) and in the field (Hanelt et al. 1997a; Gómez et al. 1998; Flores-Moya et al. 1999). While during most of the exposures to artificial UVR, the inhibition of photosynthesis was mostly a UVR and not a PAR effect (Bischof et al. 1998b, 1999; see Fig. 8-10), in studies using the natural or a simulated solar radiation, the inhibition of photosynthesis rather represents a synergistic effect of UVR and the accompanying high PAR (Hanelt et al. 1997a; Bischof et al. 1999, 2000c; Brouwer et al. 2000; see Fig. 11). For ecological considerations in the context of increasing UVB irradiances due to stratospheric ozone depletion, it is necessary to separate the inhibitory PAR and UVR effects. This is of importance as the measurable effects under exposure to high PAR or UVR are similar. Generally, decreasing maximal electron transport rates are shown to be attributed to impairment of the D_1 reaction centre protein in PS II, as well as declining carboxylating efficiency within the Calvin cycle (Mattoo et al. 1984; Ohad et al. 1984; Aro et al. 1993; Bischof et al. 2000a; see Fig. 17), while decreasing maximal quantum yields are more indicative for less efficient energy

transfer and, thus, damage to the antennae systems (Demmig-Adams and Adams 1992; Hanelt 1996).

A diagnostic feature of UVR damage is the reduction in the maximal photosynthetic rate under light saturation, either by impairment of the D_1 protein or reduced activity of Calvin Cycle enzymes, without a change in maximal quantum yield (Nogués and Baker 1995; Bischof et al. 2000a). This kind of effect is unknown in PAR induced photoinhibition (Franklin and Forster 1997). Up to now there are only indirect hints which may confirm this hypothesis for marine macroalgae. In most studies using the natural solar radiation (Hanelt et al. 1997a; Bischof et al. 2000c) or artificial radiation with a realistic UVR:PAR ratio (Bischof et al. 1999) the sharp decline in maximal quantum yield was rather attributed to the inhibitory effects of high PAR (see Fig. 11). In contrast, UVR did not further inhibit the maximal quantum yields but reduces the rate of recovery from photoinhibition (Hanelt et al. 1997a; Bischof et al. 1999, 2000c; Brouwer et al. 2000; see Fig. 11), as it is also indicative for damage to the reaction centre (Mattoo et al. 1984; Ohad et al. 1984; Aro et al. 1993). However, in many field studies conducted so far (Häder and Schäfer 1994; Hanelt et al. 1994; Franklin et al. 1996; Jiménez et al. 1998), the separate effects of PAR and UVR were not discriminated. In those studies using solar radiation, the pattern of a fast decline in photosynthetic efficiency was observed while maximal electron transport seems to be more tolerant. Thus, the adverse effects of UVR were neglected. In contrast, in many laboratory studies using an increased UVR:PAR ratio, moderate exposure to UVR is reversibly promoting electron transport (Bischof et al. 1998b, 1999; see Fig. 9). It is likely that part of the additional UVR (e.g. the far UVA) may activate photosynthesis, as the electron transport as well as the Calvin cycle capacity is not saturated under the low PAR irradiances. Blue light and far UVR is known to stimulate the thioredoxin system. By redox modification, this component is responsible for the individual fine control of the activity of several chloroplast enzymes involved in the processing and export of photosynthesis products (Scheibe et al. 1990). Furthermore, the additional involvement of a blue light receptor controlled process which may further promote even saturated photosynthetic rates can not be excluded (Schmid and Dring 1996). However, during prolonged exposure, the adverse

effects of UVR exposure prevail and may result in a reduction of maximal electron transport.

4.2.2. *UVR induced damage*

The present study has shown that exposure to UVR may result in a significant impairment of the overall photosynthetic process, however, the degree of inhibition of photosynthesis is dependent on the species and the respective state of acclimation.

In Bischof et al. 2000a, different reasons are illustrated which may lead to decreasing photosynthetic activity. The set up was designed to induce damage on different levels due to the prolonged exposure to UVR without the possibility for recovery of samples. UVR induced impairment of RubisCO and G3PDH was shown in marine macroalgae for the first time. Previous studies on higher plants stress the central role of RubisCO in UVR induced inhibition of photosynthesis (Strid et al. 1990; Jordan et al. 1992; Allen et al. 1997). Moreover, Nogués and Baker (1995) observed impairment of RubisCO to occur at lower UVR doses than impairment of primary reactions of photosynthesis. Therefore, contrary to previous studies, it is not PS II (see Renger 1986; Bornman 1989) but RubisCO that is the most critical target of UVB. However, these distinctions could not be made within our studies, due to the low resolution in time and the low sensitivity of the enzymatic assay used. It is obvious that in the tested algal species, loss of RubisCO activity is directly involved in the decrease of the maximal rate of photosynthetic electron transport. The activity of RubisCO is regulated at several molecular levels in a very complex way (see Glover 1989 for review). Therefore, one may assume that the activity of the enzyme is affected by UVR on numerous levels. Strid et al. (1990) found that it is not only the activity of the fully activated enzyme, but, even stronger, the actual activation state of the enzyme within the cell which is decreasing during UVB exposure. Additionally, the overall activity of the enzyme, as tested within our study, is also determined by its cellular concentration, which was shown to be altered due to UVR exposure (Bischof et al. 2000a; see Fig. 18, 19). Our results show clearly that loss of RubisCO activity

is due to loss of the polypeptide subunits (Bischof et al. 2000a; see Fig 18); previously, this effect has only been described for pea plants (Jordan et al. 1992) and some phytoplankton organisms (Neale et al. 1992; Lesser et al. 1996). Moreover, Jordan et al. (1992) shows that prolonged exposure may result in a lower RubisCO content due to a dramatic decrease in the mRNA transcripts encoding for RubisCO.

As shown by our results, RubisCO is much more sensitive to UVR exposure than the second Calvin cycle enzyme tested, G3PDH (see Fig. 17). The reason for the different sensitivity remains unclear. Both enzymes are of approximately similar size of about 560-600 kDa and consist of several subunits. The holoenzyme of RubisCO is composed of 8 large (51-58 kDa) and 8 small (12-18 kDa) subunits (Glover 1989); G3PDH is a hexadecamer commonly consisting of 4 complexes with each containing 2 GAP-A (approx. 36 kDa) and 2 GAP-B (approx. 39 kDa) subunits (Scheibe et al. 1996 and citations therein). Generally, the affinity of RubisCO to CO_2 is very low, therefore the RubisCO content has to be large and may represent up to 50% of the total protein content in green algae (Glover 1989). Interaction with UVR may result in a further decrease of affinity. Another aspect which determines the individual sensitivity of a protein towards UVR exposure is the respective content of aromatic amino acids, which absorb strongly in the short wavelengths range, and the number of disulphide bonds (Vass 1997). Due to UVB absorption by these components, changes in conformation and the proper function of a protein may be a consequence. Interestingly, the degradation of RubisCO subunits in *Alaria esculenta* is accompanied by the formation of high molecular weight polypeptides (Bischof et al. 2000a; see Fig. 19). This effect was previously reported from RubisCO of *Brassica napus* (Greenberg et al. 1996). The authors concluded that degradation of polypeptide subunits resulted in the aggregation of non-functioning protein complexes with a high molecular weight. However, the aggregation of protein seems to be a common response upon exposure to high doses of UVR, as a similar aggregation of high molecular weight protein complexes was also observed after exposure of lens epithel cells of squirrels (Zigman 1993). There are hardly any other data on the UVR induced impairment of enzyme activities in macroalgae. One recent study reports on the

effects of UVR on the key enzymes involved in nutrient uptake (nitrate reductase, carbonic anhydrase) in the green alga *Dasycladus vermicularis* during a daily cycle of natural solar radiation (Gómez et al. 1998). However, due to a high variation of the measured enzyme activities, conclusive evidence for specific UVR effects was not obtained in this study.

Other effects observed in the macroalgae (Bischof et al. 2000a), as well as in higher plants, include the loss of Chl *a* which is known to be a common effect of UVB exposure and may result in a decrease in photosynthetic activity (Strid et al. 1990). Moreover, a drastic decrease in overall protein content was observed in the two deep water algae tested (*Phycodrys rubens, Laminaria solidungula*; Bischof et al. 2000a; see Fig. 20). This decrease was not especially due to RubisCO degradation but affected all proteins, which may indicate an excretion of proteins into the medium, probably due to cellular damage (Tevini and Teramura 1989; Teramura and Sullivan 1994).

Lethal effects of UVR exposure were observed in brown algal zoospores (Wiencke et al. 2000; see Fig. 12). The higher UVR sensitivity of zoospores compared to adult sporophytes, was previously shown by Dring et al. (1996a). A reason for this may be the lack of photoprotective mechanisms and their limited acclimation potential to light stress (Amsler and Neushul 1991). In the present study, it was shown that the loss of viability of spores of *Laminaria digitata* partly results from damage to the DNA (Wiencke et al. 2000; see Fig. 13). Up to now there is hardly any further information available on UVB mediated DNA damage in marine macroalgae (Pakker et al. 2000), and no other data on DNA damage to macroalgal spores. Most studies on UVB induced DNA damage have been conducted on higher plants (Beggs et al. 1986) and phytoplankton (Karentz et al. 1991; Buma et al. 1995; Gieskes and Buma 1997). In phytoplankton, cell size seems to be a critical factor determining the degree of exposure of DNA to UVR (Karentz et al. 1991; Mitchell and Karentz 1993), i.e. smaller cells exhibited a greater sensitivity as compared to large cells. Therefore it is also likely that DNA of the small brown algal zoospores is particularly affected by UVR. The nanoplankton-sized flagellates were also shown to be the most sensitive phytoplankton group in terms of UVR induced impairment of photosynthesis (Häder and Häder 1989; Helbling et al. 1994; Figueroa et al. 1997). Finally,

motility of spores is also affected by UVR. The flagella apparatus of the flagellate *Euglena gracilis* was shown to be extremely sensitive to exposure to UVB, resulting in loss of motility (Häder and Häder 1988; Ekelund 1996). Brown algal zoospores, which are able to swim actively during the first 20 h after their release from the sporangia by the activity of two flagellae (Kain 1964; Makarov 1992), may be affected in a similar way.

4.2.3. *Acclimation of photosynthesis*

Due to its potentially harmful effects, exposure to UVR results in reduced photosynthetic activity. However, it is shown by Bischof et al. (1998b, 1999) and Brouwer et al. (2000) that macrothalli of brown algae are able to adjust photosynthetic performance to changes in irradiance at their respective growth site. This capability may represent one prerequisite for the algae 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; Hanelt et al. 2000a).

Within the brown algae studied, two different responses were observed in the process of acclimation of photosynthetic activity to changing radiation conditions. Firstly, the rate of recovery from UVR induced photoinhibition increases. Secondly, the degree of inhibition becomes smaller (Bischof et al. 1999; see Fig. 10). Increases in the rate of recovery may result from an activation of different repair mechanisms, counteracting the impact of UVR by a faster replacement of damaged molecules. The molecular mechanism responsible may be the same as recently 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. The mentioned studies on cyanobacteria were performed with ecologically relevant irradiances of UVB (0.2-0.8 W m^{-2}) accompanied by a low irradiance of PAR (50 µmol m^{-2} s^{-1}). However, our results show, that in algae previously acclimated to high PAR, additional UVR rather responds in a delay of the recovery process than in a further inhibition of photosynthesis (Bischof et al. 1999; see Fig. 11). This finding supports 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 UVR causing a delay in recovery (Hanelt et al. 1997a; Bischof et al. 2000c). In contrast to shallow water species like *Palmaria palmata*, UVB is shown to impair additionally photosynthesis in algae which are normally restricted to low light habitats (Karsten et al. 2000). 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 the previous studies, 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.

The second response observed in the brown algal species during acclimation to UVR 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 UVR screening compounds (Lesser 1996a). In the brown algae, phenolic compounds may contribute in

screening out UVR. It was shown for the kelp *Ascophyllum nodosum* that exposure to UVR may be a major factor controlling internal phlorotannin content (Pavia et al. 1997). However, synthesis of sufficient phlorotannin concentration may require some time before adequate shielding against UVR is achieved. Therefore, reduced inhibition might only be visible as the chronologically second response involved in acclimation. It is assumed that the formation of UVR absorbing compounds is also responsible for the decline in sensitivity to UVB in the course of the *in situ* experiment conducted by Brouwer et al. (2000).

The acclimation of parental sporophytes to higher irradiances may also be linked to spore sensitivity, when screening compounds are equally distributed to the reproductive cells. This may reflect a preadaptive capability for settling in an environment suitable for the species (Wiencke et al. 2000).

4.2.4. *UVR screening compounds*

The involvement of non-specified UVR screening compounds in acclimation to UVR exposure has been described for the kelp *Ecklonia radiata*, for the red algae *Eucheuma striatum* and *Gracilaria chilensis* (Wood 1987, 1989; Molina and Montecino 1996) and numerous other terrestrial and marine algae from Antarctica (Post and Larkum 1993). Within the red algal species, MAAs have been identified as major UVR screening substances (Karsten et al. 1998b; Sinha et al. 1998). There is evidence that the synthesis of these compounds is induced by changing irradiance conditions (Karsten et al. 1998a, 1999; Karsten and Wiencke 1999; Bischof et al. 2000b; see Fig. 14), and this seems to represent an important step in acclimation to changes in the light climate. In the Arctic endemic red alga *Devaleraea ramentacea,* a partial protection of photosynthetic electron transport, mediated by different internal MAA concentration, against UVR induced damage has been demonstrated (Karsten et al. 1999). For various marine pro- and eukaryotic organisms, MAAs may represent a defense system. In cyanobacteria, high MAA concentrations are correlated with increased resistance to UVR induced photodamage (Garcia-Pichel et al. 1993). Similar results were reported from a variety of diatoms and

from *Phaeocystis antarctica* (Riegger and Robinson 1997). In contrast, the red alga *Chondrus crispus* only exhibited an incomplete protection of photosynthetic and growth related processes mediated by MAA synthesis in response to UVB exposure (Franklin et al. 1999). Due to their optical characteristics with absorption maxima from 310-360 nm, MAAs cannot strictly serve as an UVB shield, and, hence their efficiency as a cellular sunscreen is limited to wavelengths above 300 nm, a wavelength range in which UVR absorption by cell constituents itself (DNA, proteins) is relatively low (Garcia-Pichel 1998). In contrast to the results obtained on *D. ramentacea* (Karsten et al. 1999) it was shown for *Chondrus crispus*, that MAA synthesis could also be induced by elevated levels of PAR (Karsten et al. 1998a). In other species, such as *Palmaria palmata*, a wavelength dependent stimulation of different MAAs was found (Karsten and Wiencke 1999). Moreover, there seems to be a species dependent response; therefore, patterns of MAA content may also serve as a chemo-taxonomical characteristic of a species.

The differences in internal MAA composition may be a factor involved in determining the respective sensitivity towards high levels of PAR and UVR, and thus, also reflect depth zonation of the species. This idea is supported by the results presented by Bischof et al. (2000b). The different composition and cellular concentration of MAAs in field grown *Chondrus crispus* and *Mastocarpus stellatus* and the differences in inducing MAA synthesis (Bischof et al. 2000b; Karsten et al. 1998b; see Table 1) seem to be an important factor involved in the higher resistance of *M. stellatus* towards UVR exposure (Bischof et al. 2000b; see Fig. 16). This is also reflected by its generally higher position on the shore (Kornmann and Sahling 1977, 1994). Morphologically based differences in UVR tolerance can be excluded, as both species exhibit a similar macro-morphology and histological architecture (Kornmann and Sahling 1977, 1994). However, comparative studies on these two species demonstrate a generally higher stress tolerance of *M. stellatus*. (Dudgeon et al. 1989, 1995). On Helgoland this is of particular interest, as the latter species represents a neophyte which has never been reported on the island prior to 1983 (Kornmann and Sahling 1994). Due to its generally high resistance to abiotic stress factors, *M. stellatus* has been established and dispersed all over the island. It is

reasonable to assume that this highly competitive species will prevail against *C. crispus* at locations which offer favourable conditions to both species and which are hitherto still dominated by *C. crispus*. In this context, it is important to note that samples from both species used in the experiment were collected side by side from the same shore level and, thus, under identical abiotic conditions. Therefore, apart from acclimation, also different adaptive strategies may be genetically fixed in the two species. Generally, a genetic precondition is a prerequisite for the capability of acclimation to changes in abiotic factors (Levitt 1980). This was demonstrated by the ability of different macroalgal species to synthesise UVR screening compounds (Karsten et al. 1998b).

In conclusion, three different types of adaptive strategies seem to be present in terms of capability to form UVR screening compounds (Hoyer et al. 2000): (1) deep water algae, restricted to low light habitats are generally lacking the capability to produce screening compounds (e.g. *Phycodrys rubens, Delesseria sanguinea, Ptilota plumosa*; Karsten et al. 1998b). In the lower sublittoral zone, UVR is not a natural component of the ambient light field and also surface PAR is significantly reduced (Bischof et al. 1998b). Therefore, the capability to produce screening compounds has not evolved in these species or this ability may have been lost during evolution. Additionally, it must be noted that the production of screening compounds would require additional energy costs, which may be critical, especially for low light adapted organisms, with generally low respiration rates (Kirst and Wiencke 1995). (2) In contrast, algae which grow in the upper sublittoral zone (*Chondrus crispus, Devaleraea ramentacea*; Karsten et al. 1998a, b, 1999; Franklin et al. 1999; Bischof et al. 2000b) are equipped with a basic level of screening compounds, which can be rapidly increased as soon as radiation rises. The ability for a very flexible response seems to be realised in species like *Palmaria palmata*, as different MAAs with different absorption maxima can be induced, depending on the light quality (Karsten and Wiencke 1999). (3) Finally, intertidal species like *Porphyra* sp. or *Bangia* sp. contain very high levels of screening compounds, even when exposed to low light conditions and UVR exclusion (Karsten et al. 1998b).

In contrast to the red algae, MAAs were not reported to occur frequently in brown and green algae (Karsten et al. 1998b), with the exception of the

intertidal Chlorophyceae *Prasiola crispa* containing high concentrations of MAAs (Hoyer et al. 2000). Therefore, brown and green algae might possess other UVR screening compounds. The UVR induced formation of phenolic compounds in brown algae was already mentioned above. In the green alga *Dasycladus vermicularis* from Southern Spain, the excretion of a UVR absorbing substance has been observed while specimens in tide pools were exposed to high radiation during low tide (Pérez-Roríguez et al. 1998). This substance has recently been identified as hydroxycoumarine (F.L. Figueroa, University of Malaga, pers. communication). It is possible that green algae might achieve partly UVR shielding by increasing the concentrations of carotenoids, as recently described for cyanobacteria (Götz et al. 1999).

In summary, the comparison of the species dependent ability to form UVR screening compounds under laboratory and field conditions provide strong indications for differential genetic preadaptations to the potentially harmful radiation at the natural growth site.

4.2.5. *Morphology and UVR protection*

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 UVR induced morphogenetic effects on the thalli of marine macroalgae is very limited. Very recent studies have shown that the brown alga *Alaria esculenta* grown under UVB radiation exhibits reduced growth in length and a significant increase in fresh weight, indicative for increasing thallus thickness (Michler, unpublished data). In previous studies on various Laminariales and seagrasses it was shown that thicker thalli generally exhibit a higher UVR tolerance than thin thalli (Dawson and Dennison 1996; Dring et al. 1996a; Hanelt et al. 1997b). This is also demonstrated for young sporophytes of *Alaria esculenta* collected in shallow waters. Such individuals exhibit a UVR induced inhibition of

photosynthesis, which is comparable to the response of large sporophytes taken from 11 m water depth (Bischof et al. 1998b).

4.2.6. *Algal response to other stress factors*

Is a higher tolerance to UVR accompanied with a higher tolerance to other abiotic stressors, especially in species inhabiting variable environments such as the eulittoral and upper sublittoral zone (Davison and Pearson 1996)? In the study by Bischof et al. (2000b), the higher UVB tolerance of *Mastocarpus stellatus* compared to *Chondrus crispus* from the same shore level was shown. Differences between these species were also demonstrated for other stress factors, such as temperature, desiccation and freezing, suggesting a generally higher stress tolerance in *M. stellatus* (Mathieson and Burns 1971; Dudgeon et al. 1989, 1995). The formation of MAAs may, therefore, be part of a general stress response rather than a specific reaction to exposure to UVR. Apart from their role as screening substances, which are shown to be induced from UVB to the blue waveband (Karsten et al. 1998a, 1999; Franklin et al. 1999), it has been shown in Antarctic red algae, cultivated under only low levels of PAR, that these species synthesise MAAs, in response to a moderate increase of PAR (Hoyer, unpublished data). Moreover, MAAs were found to provide also protection against photooxidative stress in algal tissue (Dunlap and Shick 1998) and may act as osmotic solutes (Oren 1997). The increase of the phlorotannin content in brown algae is induced by UVB exposure (Pavia et al. 1997), but also by herbivory (Steinberg and van Altena 1992; Pavia et al. 1997; Pereira and Yoneshigue-Valentin 1999). Moreover, the excretion of hydroxycoumarine by *Dasycladus vermicularis* (Pérez-Rodríguez et al. 1998) has not only been observed under high irradiances during low tide, but also in laboratory studies under low irradiances of PAR, in response to rising temperature, changing pH, and decreasing salinity (F.L. Figueroa, University of Malaga, pers. communication). In addition, reactive oxygen species (ROS) are known to be generated under various kinds of environmental stress, including UVR, high PAR irradiance, elevated temperatures and drought as well as

nutrient limitation (Asada and Takahashi 1987; Lesser 1996b). In this context, it is interesting to note that in higher plants, ROS have been identified to be important components of the signal transduction pathway leading to the down-regulation of photosynthetic genes in response to UVB (Mackerness et al. 1999). In contrast, for a specific protective response exclusively to UVB, its detection would be a prerequisite. In higher plants, the presence of a UVB specific photoreceptor has been reported, acting to mediate photo-morphogenetic effects in response to UVB exposure (Barnes et al. 1996), but no information is available for macroalgal species. However, brown algae seem to be able to perceive blue light and UVA as an environmental signal, triggering carbon acquisition (Schmid and Dring 1996) as well as chloroplast movement (Pfau et al. 1988; Hanelt and Nultsch 1989).

4.2.7. *Protection against high PAR*

While most strategies protecting against the harmful effects of UVR also provide protection against high PAR (e.g. increased thallus thickness, screening compounds, antioxidative defense), there are various strategies of photoacclimation, which are only effective in the PAR range (Falkowski and LaRoche 1991). In brown algae, it has been demonstrated that chloroplast movement contributes to the protection of the photosynthetic apparatus against excess radiation (Nultsch and Pfau 1979; Pfau et al. 1988; Hanelt and Nultsch 1990, 1991), but this mechanism has limited effect in the UVR region due to the strong scattering within the cell (Hanelt and Nultsch 1989). Physiological mechanisms of short term photoacclimation against over-reduction of the photosynthetic apparatus (e.g. dynamic photoinhibition by increasing non-photochemical quenching mediated by the action of the xanthophyll cycle, and state transitions) are hitherto only described to be active under high PAR (Dau 1994; Osmond 1994; Uhrmacher et al. 1995; Schofield et al. 1998). Reducing the absorption cross section is also a common response of plants exposed to high irradiances of PAR (Niyogi 1999). Amongst other mechanisms, this can be achieved by the alteration of pigment composition due to the increase of the

relative amounts of carotenoids which do not transfer excitation energy to the reaction centres, while overall pigment content decreases (Falkowsi and LaRoche 1991, Stengel and Dring 1998). However, this may also partly contribute to the protection against UVR as increased carotenoid concentrations can act as UVR screens as well as quenchers of generated ROS (Jialal et al. 1991; Day et al. 1992; Götz et al. 1999).

4.3. Ecological implications

Due to the high variability of the natural radiation climate and the flexible response of macroalgae to UVR, the ecological consequences of enhanced ozone depletion are still difficult to predict. There are hardly any data available on UVR effects on the organism, community or even at the ecosystem level. The first study of UVB effects on Arctic macroalgae *in situ* was conducted by Brouwer et al. (2000). With respect to the ecological consequences of ozone depletion, three points are of particular interest, (1) the impairment of macroalgal growth and, thus, the production rate of the algal communities as well as of the whole ecosystem, (2) the impairment of reproductive success, (3) the changes in species composition and depth zonation.

4.3.1. *Growth and productivity*

Throughout the present study, it is shown that all species which do encounter UVR in the field (i.e. the species inhabiting the intertidal and the upper sublittoral zone) possess different mechanisms for acclimation to respond to changes in light climate (Bischof et al. 1998b, 1999, 2000b; Brouwer et al. 2000; Karsten et al. 1999). In particular, the capability for a fast acclimation as demonstrated in *Alaria esculenta* (Publ. 3) is an important prerequisite to cope with the drastic changes in irradiance during the transition from Arctic winter to spring/summer. Acclimation responds to an increased level of PAR but also protects photosynthesis against UVB (Bischof et al. 1998b; Karsten et al. 1999).

In this study, the potentially protective effects are only documented by measuring changes in photosynthesis. However, in an ecological context these measurements are in-sufficient to describe long term effects (Cordi et al. 1997). Recent laboratory experiments on the cold temperate red alga *Chondrus crispus* reveal that prolonged UVR exposure results in a stepwise reduction in the degree of inhibition of maximal quantum yield of photosynthesis and pronounced MAA formation (van de Poll, unpublished). After some days in the UVR treatment, the algae exhibit only small reductions of Fv/Fm, which are rapidly reversible as soon as UVR is switched off. There is a significant reduction in growth rates, accompanied by detectable levels of thymine dimer formation, indicative of DNA damage. This shows clearly, that UVR does exert adverse effects which are not necessarily reflected by a reduced photosynthetic activity. In field studies, other biological processes, such as nutrient uptake by the macroalgae *Ulva lactuca* and *Fucus vesiculosus*, were sensitive to UVB (Döhler et al. 1995). This is of particular interest, as these species occur mainly in the eulittoral zone and should therefore be especially resistant to UVR stress. Moreover, photosynthetic quantum yield in other species of the generae *Fucus* and *Ulva* has been shown to be minimally affected by natural UVB radiation (Hanelt et al. 1997a; Brouwer and Kromkamp 1999; Bischof et al. 2000c). 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. However, *in situ* growth experiments revealed hardly any adverse effects under present UVB levels (Aguilera et al. 1999; Altamirano et al. 2000a, b; Brouwer et al. unpublished data). Aguilera et al. (1999) and Brouwer et al. (unpublished) conducted similar growth experiments on *Laminaria* species in the Arctic Kongsfjord at different depths. However, no UVB induced impairment of growth was detected, which might partly be due to the strong absorption of UVB in the water column (Hanelt et al. 2000a). In contrast, in experiments of artificially increased irradiance, either by transplanting algae from deep to shallow water or by supplementary UVR from fluorescent tubes, most species were affected on growth (Grobe and Murphy 1994; Han 1996a, b; Aguilera et al. 1999). Therefore, a reduction of macroalgal productivity in response to increased UVB levels in future cannot be excluded.

4.3.2. *Reproductive success*

There are only few data available on the UVR induced impairment of reproductive success. Wiencke et al. (2000) demonstrated that brown algal zoospores respond very sensitively towards artificial UVR exposure and that photosynthesis of zoospores is much more sensitive than of adult sporophytes being exposed to the same doses of UVR. Moreover, significant thymine dimer formation was detected in the DNA of zoospores from *Laminaria digitata* under irradiances which do not induce detectable levels of DNA damage in the adult sporophytes (Wiencke et al. 2000; H. Pakker, University of Groningen, pers. communication). Dring et al. (1996a) and Hanelt et al. (1997b) showed that zoospores and the microscopic gametophytes of *Laminaria* species are particularly sensitive to UVR stress, which may either limit reproductive success (by increasing zoospore mortality), and in turn, influence macroalgal zonation patterns, as spores are not able to establish at locations where ambient radiation impairs viability. This relationship was demonstrated for Laminarian species in Southern Spain (Wiencke et al. 2000), where biologically effective irradiance down to 7 m water depth excludes the establishment of zoospores.

4.3.3. *Depth distribution*

In a large number of studies it was demonstrated, that the species sensitivity to solar radiation stress is a function of depth distribution (Dring et al. 1996; Larkum and Wood 1993; Hanelt et al. 1997a, c; Hanelt 1998; Bischof et al. 1998a; Yakovleva et al. 1998; Karsten et al. 2000). Moreover, some authors regard solar UVR as one of the most important factors controlling the upper distribution limit of macroalgae in the field (Maegawa et al. 1993). Therefore, it is reasonable to assume 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. As several acclimation processes can counteract radiation stress, this scenario is still questionable, especially in areas characterised by higher water turbidity, such as coastlines (Hanelt et al. 2000a).

In the tropics, at higher water transmittance, UVR does penetrate deeper into the water column, but UVR levels are not expected to change due to ozone depletion. The results presented by Wiencke et al. (2000), strongly support the idea that UVB can affect zonation patterns via the high UVR susceptibility of zoospores, thus preventing recruitment in shallow waters with high UVR irradiances. Through this process, elevated UVB may result in a shift of macroalgal communities to deeper waters.

4.3.4. *Summary of present conditions*

In conclusion, a diagram is presented to summarise the response of macroalgae to solar UVB under the presently observed and expected future radiation conditions (Fig. 21). It is illustrated, how the primary molecular effects of UVB absorption may lead to changes in ecosystem structure.

Under present radiation conditions, UVB radiation has already to be regarded as a common abiotic factor, which influences the physiology of Arctic macroalgae. However, its potential threat to biologic processes is counteracted by several adaptive strategies activating different protective 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. The results are recovery from UVB induced inhibition of photosynthesis, and the equilibrium between the rate of UVB induced DNA damage and its repair under the respective radiation conditions. As part of all abiotic factors, UVB induced physiological effects contribute to actual growth rates and the reproductive success of algae. *Vice versa*, growth rates are directly connected to the development of protective mechanisms, as the establishment of adaptive strategies requires additional energy costs. Growth and reproduction directly influence the population of the species, and hence, ecosystem structure.

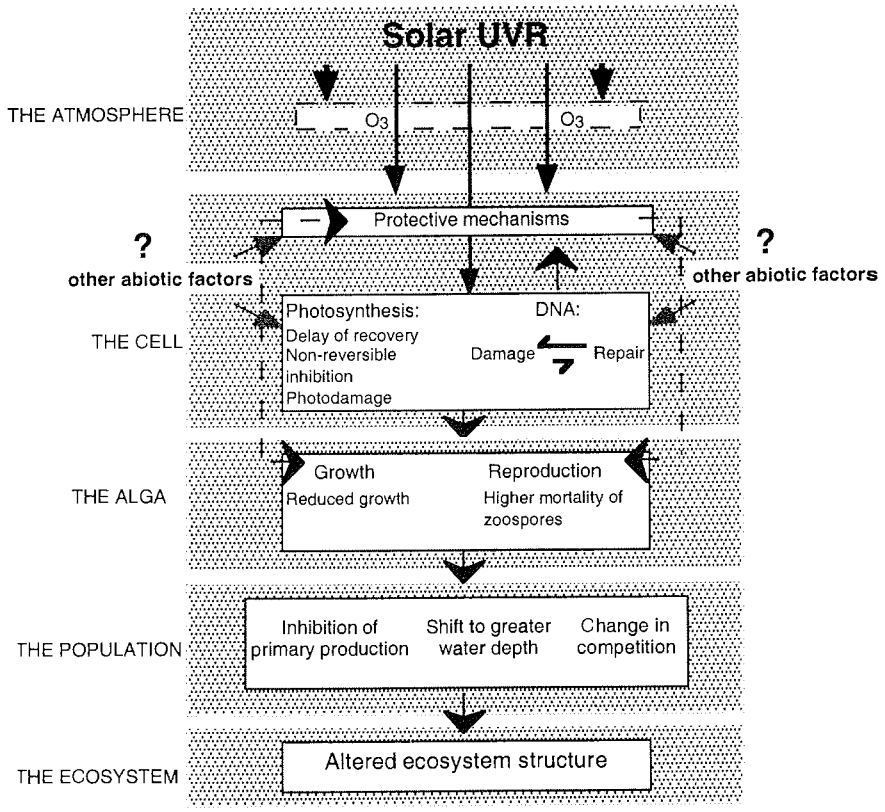

Fig. 21: Response of macroalgae to elevated levels of UVB radiation; UVR ← , other abiotic factors ← , algal reactions ←

4.3.5. *Outlook to future conditions*

In the context of global climate changes, the acclimation potential of the algae is of particular importance. Further decreasing stratospheric O_3 concentration will enhance UVB radiation on the earth's surface, and it is still not known if the capability of species to optimise protective mechanisms can keep pace with the increase in the UVB irradiance.

Protective mechanisms, which presently encounter radiation stress may not be capable to adequately respond to elevated UVB levels. Possible consequences are that the rate of DNA damage exceeds the rate of repair and

that the delay of recovery from inhibition of photosynthesis may turn into a non-reversible impairment of photosynthesis and, consequently, result in the destruction of the photosynthetic apparatus. These effects will certainly impair growth and reproductive success. Moreover, the need to improve protection will require additional energy costs, which might reduce algal growth and productivity further. The actual situation in Southern Spain demonstrates that UVB can exclude the settlement of brown algal zoospores of certain species in shallow waters (Wiencke et al. 2000). Increases in UVB levels may therefore result in a shift of sensitive species to greater water depth, thereby affecting ecosystem structure.

The time period required for sufficient adaptation to respond to ozone hole conditions is a critical step. If sufficient acclimation is possible to be achieved by alterations in the phenotype of algae, elevated UVB levels will only have few aut- and synecological consequences. However, if changes in the genotype are necessary to adequately respond to higher UVB levels, the required time for adaptation will take longer and the possible consequences might be most severe (Sisson 1986).

4.4. Concluding remarks and future perspectives

This study was directed to answer some basic questions related to macroalgal physiology and UVR exposure. The results clearly show that UVR has the potential to adversely affect the macroalgal community in the Arctic and, thus, also ecosystem structure. Although it is demonstrated that photosynthesis in all species studied was sensitive to UVR exposure, effective acclimation strategies are present in different species (Bischof et al. 1998b, 1999, 2000b; Karsten et al. 1999; Brouwer et al. 2000), reducing the harmful effects of UVR at the natural growth site. Deep water algae, which were shown to be very sensitive to UVR (Karsten et al. 2000) miss acclimation and protective mechanisms against UVR, as it is not a natural component of the ambient light field (Bischof et al. 1998b; Hanelt et al. 2000a). Cultivated material exhibited that, apart from acclimation, a genetic preadaptation is a prerequisite to

encounter efficiently UVR stress (Bischof et al. 2000a), however, the physiological basis of this remains to be elucidated in further studies.

These results offer various aspects on which future research should be directed. From the obvious capability of brown algae to adjust photosynthesis to changes in ambient radiation, demonstrated by Bischof et al. (1998b, 1999), the question arises, what are the physiological and molecular bases of these effects. Strategies like sunscreen production (as shown by Karsten et al. 1999) should be further investigated to determine the internal trigger of the protective mechanism and, in the case of MAAs, the basic pathway of their formation. To be able to respond to UVR, the perception of the changes in light climate is one important prerequisite. Recent studies, which were directed to clarify the signal transduction pathway involved in UVR response of higher plants (Mackerness et al. 1999), should be necessarily applied to macroalgal research. However, apart from this physiological approach, future studies should also be further directed to ecologically relevant aspects. In laboratory studies, the effects of the respective UVR wavelengths which increase due to ozone depletion, should be dissected more carefully. Moreover, more realistic scenarios of ozone depletion in the laboratory have to meet outdoor radiation conditions, which, of course, are difficult to simulate (Thiel et al. 1996). Therefore, the development of sunlight simulators which allow research also on macroorganisms will be a challenging task in future UVR research.

It is necessary to undertake field research whilst trying to elucidate the ecological consequences of enhanced ozone depletion. Long term *in situ* measurements must be conducted under elevated UVB levels. Such studies have already been successfully conducted in Subarctic terrestrial ecosystems (Gehrke et al. 1995; Johansson et al. 1995b), and should be applied also to macroalgal research, although installing the set-up on the shore will bear difficulties. In this context, mesocosm experiments may be a good compromise to meet natural solar radiation conditions with artificial change of abiotic parameters. Two major points have to be stressed in field experiments: (1) the first is the need for real *in situ* growth measurements to estimate how future ozone depletion will affect productivity on the ecosystem level, (2) the second one is the investigation of the most sensitive establishment stages (e.g. spores,

germlings) to be able to predict possible changes in macroalgal zonation patterns due to enhanced UVB radiation (Wiencke et al. 2000). As acclimation and protective mechanisms counteract adverse effects of UVB in the field, it is evident that long term experiments, which are still lacking not only for Arctic species, must be conducted. Investigations of tropical species, which are permanently exposed to high radiation levels may provide further insight into adaptive strategies. Finally, the interaction of UVR with other stress factors in marine macroalgae remains to be studied. This is of particular interest, as in addition to UVB, water temperatures are also likely to increase due to global warming. UVR research in Arctic macroalgae is still important in terms of basic physiological research as well as ecological monitoring, and will provide further knowledge on the functioning of the unique Arctic coastal ecosystem.

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