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Seaweed Biology

Novel Insights into Ecophysiology, Ecology and Utilization

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Preface

Two thirds of the world are covered by oceans, whose upper layer is inhabited by photoautotrophic organisms, known as algae. Within coastal ecosystems, marine seaweeds have been identified as a group of organisms of vital importance for ecosystem function. On rocky coasts, they form vast underwater forests of considerable size with a structure similar to terrestrial forests and provide diverse habitats and breeding areas for an uncountable number of organisms including fishes and crustaceans. They are an important food source not only for numerous herbivores, such as sea urchins, gastropods, and chitons, but also for detritivores such as filter feeders and zooplankton, which are feeding on degraded seaweed biomass and on energy-rich spores released in vast quantities from seaweeds. On beaches in some localities large masses of seaweeds are stranded and support meiofauna species.

Although marine seaweeds and seagrasses, altogether known as macrophytes, cover only a minute area of the world's oceans, their production amounts to 5–10% of the total oceanic production. Carbon assimilation of kelps, large brown algae of the order Laminariales, is with 1.8 kg carbon m^{-2} $year^{-1}$ similarly high as that of dense terrestrial forests and even exceeds the primary production of marine phytoplankton up to ten times.

Seaweeds are not only of high ecological, but also of great economic importance. Dried thalli are directly used as human and animal food and also as fertilizer. Extracted seaweed substances are used as stabilizers and stiffeners in food industry, cosmetics, pharmaceutical industry, and biotechnology. In future, aquaculture of seaweeds will certainly strongly intensify, especially in integrated multi-trophic aquaculture systems making use of the waste products or biomass generated by other organisms in the system. Industrial use of seaweeds will also strongly increase as basis for CO_2-neutral production of ethanol and methanol as biofuels.

Seaweeds are exposed to a variety of external factors, which affect their physiological and ecological performance. This suite of factors is, however, not constant, but changes along different timescales. There are short-term daily fluctuations of abiotic factors, especially in low latitudes, whereas in high latitudes seasonal variations are dominating. Long-term changes related to the climate history of the earth extend over thousands and millions of years. But changes do not only have natural reasons. In the younger history of the earth man-made changes became evident on a local and global level. An important local change is for example eutrophication of estuaries, bays, and side oceans. With respect to global changes, the burning of fossil fuels leads on the one hand to global warming through the greenhouse effect and on the other hand to ocean acidification through CO_2-mediated changes on the seawater carbonate system. Stratospheric ozone depletion results in an increase of UV-B radiation at the earth's surface and in the upper layers of the oceans. If the acclimation potential of an individual seaweed species is high, this species might not strongly be affected by external changes. In contrast, in species, which are more strongly (genetically) adapted to a special suite of external factors, the effects will be more prominent. So, on the level of communities variation of each of these factors can change the achieved ecological equilibria between the species, and can finally also prompt economic consequences.

This book is a collection of articles summarizing the advances of seaweed biology achieved within the last decades and also pointing to overlooked treasures. The overall aim of this book is to complement available textbooks for advanced students and young researchers. The book contains 22 chapters, written by experts in the various research areas. The chapters are grouped into five parts.

The first part of the book covers fundamental processes and acclimation strategies of seaweeds toward the abiotic environmental variables. Acclimation to limiting and excessive light conditions is considered in Chap. 1 by *D. Hanelt* and *F.L.-Figueroa*. Changes in pigment composition in response to different underwater spectra and the use of light as environmental signal are also discussed. In Chap. 2 by *I. Gómez* and *P. Huovinen*, the adaptations to incorporate and process dissolved inorganic carbon are summarized. An important part of this chapter deals with morpho-functional aspects of carbon metabolism, in particular with the role of storage carbohydrates, thallus anatomy, and long-distance transport of photoassimilates and patterns of carbon allocation, important features e.g. for supporting seasonal development. *A. Eggert* focuses on phenotypic acclimation to temperature outlined in Chap. 3. Here, disruptive temperature stress and thermal tolerance is another focus, before the prime role of temperature for the determination of geographic distribution is discussed. In this respect, this chapter sets the basis for Chap. 18 by *I. Bartsch* et al. who elaborate on the shift of marine phytogeographic regions under conditions of global warming. In Chap. 4, *F. Gordillo* reviews the relationship between algal nutrition and their environment in order to better understand how seaweeds meet their nutritional needs including the uptake of inorganic carbon. *U. Karsten* (Chap. 5) discusses the effect of salinity stress and desiccation on the physiology of seaweeds and the involved metabolic processes during osmotic acclimation. In Chap. 6, *K. Bischof* and *R. Rautenberger* summarize the processes involved in the generation of reactive oxygen species (ROS) during environmental perturbations, their effects on seaweed performance, and the respective antioxidative strategies against photosynthetically formed ROS. At the end of the chapter pathogen defense through oxidative bursts is discussed.

Part II focuses on the multitude of biotic interactions found in seaweed communities. The first chapter in this part (Chap. 7) by *M.S. Edwards* and *S.D. Connell* addresses competition as a major factor structuring seaweed communities. Along that line *K. Iken* discusses grazer–seaweed interactions as other major drivers for seaweed standing biomass and community composition, for the energy flow through the system, and with respect to higher trophic level predator–prey interactions (Chap. 8). Chapter 9 by *C.D. Amsler* summarizes our present knowledge on seaweed chemical ecology with emphasis on sensory and defensive systems. Hitherto, the microbial community populating seaweeds and, thus, potentially affecting algal growth or secondary epibiosis is still understudied: In Chap. 10 *M. Friedrich* summarizes the advances in metagenomic approaches to address seaweed–bacterial associations. The topic of epibiosis is taken further in Chap. 11 by *P. Potin* who addresses recent insights into the interactions of seaweeds with their epi- and endophytes, as well as with their parasites. The problems related with invasive marine seaweeds are presented in Chap. 12 by *N. Andreakis* and *B. Schaffelke*. The increasing number of marine invasions is mainly due to intensified shipping and global environmental changes. Moreover, many invasive seaweeds are commercially used, but risks are high and strategies are needed to control intentional and accidental introductions.

In Part III, the reader is introduced into structure and function of the main seaweed systems of the world. The first chapter in this part, Chap. 13, by *C. Wiencke* and *C.D. Amsler* focuses on seaweeds and their communities in polar regions. Biodiversity, biogeographical relationships, ecophysiological characteristics of individual species, and ecology of polar seaweed communities are considered here. The cold-temperate seaweed communities of the southern hemisphere are addressed in Chap. 14 by *P. Huovinen* and *I. Gómez*. To our knowledge, this is the first comprehensive overview covering the southwestern and southeastern South American region, the Victoria-Tasmania region, the southern New Zealand region, and the sub-Antarctic Islands region. After an introduction of these regions and their basic abiotic environmental settings, structure and function of the respective communities, as well as biogeographical processes, are discussed. As an example for the warm-temperate region the largely understudied deep-water kelp forests of the Alboran Sea (SW Mediterranean Sea) and the Strait of Gibraltar are presented in Chap. 15 by *A. Flores-Moya* focusing in particular on growth and reproductive strategies in context to the prevailing abiotic factors. The role of seaweeds in tropical marine coastal systems is discussed in Chap. 16 by *A.Y. Mejia* et al. In these systems, seaweeds are not the dominant habitat providers but are important with respect to reduction of nutrients, provision of food, and refuge for predators and prey. However, excessive growth can lead to complete regime shifts, threatening the stability of the entire coastal system. An overview on the ecology of floating seaweeds and their communities is given by *E. Rothäusler* et al. in Chap. 17. Floating seaweeds can bridge large distances especially at high latitudes where the algae can compensate grazer-induced tissue loss by relatively high growth rates at the prevailing temperatures. In this way, seaweed floes may act as important vectors of dispersal for the associated invertebrate fauna.

Part IV contains a compilation on the effects of global and local environmental changes on the performance of seaweeds and their communities. In Chap. 18, *I. Bartsch* et al. identify expected distributional shifts of major biogeographical regions under conditions of global warming using a macro-ecological modeling approach. According to their results, the tropical regions will expand considerably and all other regions, except the Antarctic region, will extend toward the poles. Along with the shift of the biogeographical regions, the community structure at the boundaries will also dramatically change along vast coastlines. Increasing carbon dioxide (CO_2) concentrations in the atmosphere do not only result in global warming, also the pH of the world's oceans is lowered, a process called ocean acidification. This phenomenon is presented in Chap. 19 by *M.Y. Roleda* and *C.L. Hurd*. The consequences of ocean acidification can affect seaweeds from the cellular to the community level. Particularly important are the interactive effects with other factors, e.g., global warming, eutrophication, and ultraviolet radiation (UVR) due to stratospheric ozone depletion. The latter effect on seaweeds is discussed in Chap. 20 by *K. Bischof* and *F.S. Steinhoff* not only with respect to the damaging effects of UVR, but also to the acclimation strategies and the adaptive traits of seaweeds exposed to UVR. Special attention is given here to the microscopic developmental stages of seaweeds. A rather locally acting, but nonetheless very severe environmental impact is eutrophication, which is addressed in Chap. 21 by *M. Teichberg*. This contribution provides an overview over eutrophication-induced formation of macroalgal blooms and their ecological consequences. Moreover, shifts in macroalgal growth in shallow estuaries, coral reefs, and intertidal or subtidal rocky shores are discussed in order to understand how different systems may contrast in response to shifts in top-down versus bottom-up control.

The final part provides a comprehensive overview on recent developments in seaweed aquaculture, industrial applications, and the overall economical importance of seaweeds. This information is incorporated in Chap. 22 by *C.M. Buchholz* et al.

For sure, the present volume of the 'Ecological Studies' presented is far from being completely covering all aspects effective on and affected by seaweeds in its entirety. However, a review on the respective concluding remarks stated by contributing authors at the end of the respective chapters allows for the identification of the most important gaps in knowledge and invaluable insights into future research priorities with respect to seaweed biology.

It is evident that there is still a need for studies on the fundamental adaptational features allowing seaweeds to thrive in their respective environments. This holds especially true for species inhabiting somewhat extreme habitats, like intertidal systems, or polar areas. Newly developed methods in molecular physiology need to be implemented also in seaweed biology on a large scale. In this respect, more studies in gene expression responses following transcriptomic approaches will be promising tools and will revolutionize our understanding of seaweed responses to the environment. *In concreto*, more profound studies on the fundamental strategies of adaptation are urgently needed for example for addressing life strategies of Arctic kelp to understand the triggering of light vs. dark metabolism in extremely seasonal habitats. Hitherto, dark metabolism of kelp, which needs to be sustained under conditions of the polar night and additional sea ice cover, is just fragmentarily understood.

The enforced implementation of molecular tools will also ease our endeavors to predict seaweed responses to environmental change. Along this line molecular analyses should also go beyond gene expression and also aim at the understanding of sensing of environmental cues and identify signal transduction pathways. Genomic, proteomic, and metabolomic studies will become more prominent in seaweed research, facilitated by past, present, and future whole genome sequencing projects. The completion of the *Ectocarpus* genome project in the year 2010 represented a new ignition to seaweed-related research activities, and the currently ongoing *Chondrus* and *Porphyra* genome project will result in another boost in research. Based on their prime ecological significance to coastal ecosystem function, we propose that dominant species of kelp, e.g., *Macrocystis pyrifera, Laminaria hyperborea* should be considered as upcoming candidates in such sequencing projects.

A second priority of future research on seaweeds may be described by the buzzwords "integration" and "interaction": In their environment seaweeds are exposed to a complex set of abiotic and biotic variables, which may change independently or interdependently. Factors may interact synergistically or compensatory. Studies aiming to predict consequences of environmental change in seaweed communities have to consider the interaction of (multiple) stress factors more thoroughly and conceptualise multifactorial experiments. Furthermore, the different life histories of the species under investigation need to be integrated more strongly in environmental stress physiology. In this respect, it is important to identify the life history stage most susceptible to the impinging environmental stressors, as this will represent the bottleneck for reproduction, recruitment, and thus, population structure. Stage-specific acclimation capacities have to be addressed in order to define thresholds of stress, biogeographical boundaries, and the so-called tipping points, which will be important to define with respect to resilience. Furthermore, also biotic factors largely interact, and changes in interspecific interaction may be both the outcome and the cause of environmental stress susceptibility. The multiple interactions between seaweeds and their grazers, foulers, parasites etc. offer a hitherto largely understudied field of interspecific sensing and signaling. Again, these studies should be linked to transcriptomic and metabolomic approaches.

In an era of climate change, these approaches should be integrated by modellers in order to increase the predictability of consequences of environmental disturbance. Climate modellers, physical oceanographers, and seaweed ecophysiologists need to team up in order to outline scenarios of future seaweed community and coastal ecosystem functions. As climate change will strongly affect biogeographical boundaries, future studies on the dynamics, range expansion, connectivity, and ecotype formation of populations will be most important. In a concrete example, there are current indications for ecotype formation in *Laminaria* at Arctic and cold-temperate sites, respectively, which might be reverted in the future due to the predicted process of atlantification of Arctic regions. Improvements in the molecular tools applied in population genetics should then also be used to increase our knowledge in invasive species ecology as well as to understand the significance of kelp rafting to species dispersal.

The improvements in analytical techniques applied in studies on seaweed biology are paralled by the increasing efforts for seaweed uses for economic purposes. Apart from the potentially innumerous pharmacological effects seaweed-derived compounds may confer, the use of seaweeds as bioabsorbers of aquaculture effluents has a great application potential. The increasing applied sector in seaweed biology directly relates to further study questions related to conservation and socio-economy.

Climate change in its different manifestations and facets on global and regional scales, the rapidly increasing anthropogenic pressures on coastal areas, as well as the vastly growing demand for alga-derived products, represent challenges to both human society in general and seaweed biologists in particular. Hitherto, it is commonly accepted that the ecological and economical values of seaweeds can hardly be overestimated. Against this background there is an increasing need for integrated studies on seaweed biology, stretching from molecular physiology to community ecology and even further to societal aspects. Along this line, we hope that this book will further increase the awareness of the enormous ecological significance of seaweeds in coastal environments.

Bremerhaven and Bremen Christian Wiencke and Kai Bischof

Contents

Part III Structure and Function of the World's Main Seaweed Systems

Part IV Effects of Global and Local Changes on the Performance of Seaweeds

Part V Aquaculture and Economical Importance of Seaweeds

Part I

Fundamental Processes and Acclimation to Abiotic Environmental Variables

Chapter 1
Physiological and Photomorphogenic Effects of Light on Marine Macrophytes

Dieter Hanelt and Félix López Figueroa

1.1 Introduction

The coastal zone of the marine habitat is exposed to considerable diurnal changes in solar radiation due to the position of the sun, clouding and, especially, the tides. Thus, these temporary changes in the costal environment can appear much stronger compared to terrestrial habitats. Whereas algae in air or the upper littoral zone are supplied with sufficient or even with an excess of radiation energy (Wilhelm and Selmar 2011), in deeper regions of the euphotic zone light is clearly limiting for seaweed growth. It is a reason why seaweeds generally need to grow on the continental shelf (epipelagic), down to a maximal depth where the light level is not lower as 0.05% or 0.001% of the surface irradiance in the tropics (Lüning 1990). Moreover, conditions in the coastal areas are quite different compared to the open ocean as in coastal zones generally an inflow of freshwater occurs which can be loaded with sediments. Penetration of solar radiation into the water body is largely determined by scattering and absorption of biological and inorganic material, with higher concentrations in coastal areas. Coastal waters show large temporal changes and regional differences in the concentration of dissolved and particulate matter influencing temporal penetration of solar radiation. This is the basis on which Jerlov (1976) classified marine waters into nine types of coastal and five types of oceanic waters in dependence on the respective transmittance characteristics.

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1.2 Photosynthesis Under Limiting Light Conditions

Sublittoral species growing in deep water must be adapted to chronic low light. For planktonic algae, generally a lower depth limit of 1% of the surface irradiance is regarded as defining the euphotic zone (Steemann Nielsen 1975), and this limit can be even 0.1% for picoplankton in oceanic waters. Seaweeds of the order *Laminariales* reach their lower growth limit at about 0.6–1.2% of surface light, whereas for some deep growing rhodophytes a minimum of 0.001–0.05% was determined (Lüning 1981, 1990). The photosynthetic rate of different *Laminaria* species exceeds the respiratory rate and thus the compensation point (E_c) at about 5–8 μmol m^{-2} s^{-1}, whereas in deep water red algae an irradiation of about 2 μmol m^{-2} s^{-1} is already sufficient (Lüning 1981). Deepest crustose macroalgae seem to survive at an absolute light minimum of about 0.01 μmol m^{-2} s^{-1} (Littler et al. 1986). These red crustose corallines show a large light absorptance and employ light-harvesting pigments with a high energy-cost in their production per unit light absorption rate in a given underwater spectrum (Raven and Geider 2003). Raven et al. (2000) outlined that it is difficult to explain growth of algae below 0.5 μmol m^{-2} s^{-1} as there are energy-consuming reactions which use an increasing fraction of energy input when photon flux density decreases. Among these processes are redox back reactions of reaction center II, the leakage of H^+ through thylakoid membranes and the turnover of photosynthetic proteins. The first of the two processes limit the rate of linear electron transport and ADP phosphorylation, while the latter consumes ATP. Thus, it is not yet clear how crustose red algae can grow down to 274-m water depth where the average incident photon flux density for 12 h day^{-1} does not exceed 0.02 μmol m^{-2} s^{-1} (Raven and Geider 2003).

Low light adapted species are typically characterized by high photosynthetic efficiencies and very low light compensation (E_c) and saturation points (E_k), ranging between 1 and 15 and between 14 and 52 μmol photons m^{-2} s^{-1}, respectively (Dunton and Jodwalis 1988; Wiencke et al. 1993; Weykam et al. 1996; Brouwer 1996; Eggert and Wiencke 2000).

For a certain time period net photosynthetic rates need to be high enough that seaweeds can promote growth, reproduction, as well as enough energy storage to cope with reduced light availability also during the winter season. Using data on daily changes of in situ irradiance and P–E derived parameters such as photosynthetic capacity (P_{max}), dark respiration, E_c and E_k, it is possible to calculate the daily periods over which carbon (C) assimilation exceeds C losses due to respiratory activity at different water depths. This metabolic C balance is regarded to determine the lower distribution limit of algae. Due to low E_k values, species from King George Island (Antarctica) are exposed during spring–summer for periods ≥12 h day^{-1} at about 20 m depths to irradiances above saturation (period of saturation H_{sat}). Under these conditions, species such as *Palmaria decipiens* or *Desmarestia anceps* achieve positive C balances about 3 mg C g^{-1} FW d^{-1}. At 30-m depth daily light availability decreases to values between 7 and 9 h in summer, but C balance is still positive in 4 of 5 studied species (Gómez et al. 1997).

Only in the case of *Desmarestia anceps* from 30 m, a negative C balance was determined, indicating that at this depth the alga is at its lower distribution limit. In contrast, *P. decipiens, Gigartina skottsbergii* and *Trematocarpus antarcticus* and especially *Himantothallus grandifolius* are metabolically able to grow even in deeper waters which mean they have very modest requirements.

Under low light conditions higher pigment content within the thalli was observed as under strong light conditions (Ramus et al. 1976, 1977). The chance of photon absorption increases with increasing photosynthetic antenna size. Algae collected from or transplanted to different water depths show that the content of accessory pigments increases with lower light conditions in deep waters (Lüning 1990), e.g., in green algae the chlorophyll *a:b* ratio decreases demonstrating especially the increase of the antenna size of the photosynthetic apparatus (Yokohama and Misonou 1980). Whereas under low light conditions in deep water a larger antenna size increases the capacity of light absorption, a smaller antenna helps to avoid photoinhibition and photodamage due to over excitation under high light conditions close to the water surface or during emergence at low tide. Under low light conditions the plant invests more energy in the synthesis of light-collecting pigments and in strong light into the synthesis of photosynthetic enzymes, electron chain components as well as photo-protective structures and energy-dissipating mechanisms.

A study of Marquardt et al. (2010) showed that the saturation point E_k of all red algal species tested decreased with increasing depth concomitantly with the decreasing light availability. This may be due to the adjustment of the photosynthetic apparatus itself via changes of the reaction center ratio, changes of the relative size of the light-harvesting complex (LHC) or changes in the relative content of light protective pigments. Changes in thallus morphology are another possibility to achieve acclimation, e.g., change of thickness, branching, length, density of photosynthetic units (Küster et al. 2004). Johansson and Snoeijs (2002) demonstrated by measurements of photosynthesis versus irradiance curves (PE curves) that light-saturated net photosynthetic rates (P_max), respiratory rates in darkness (R_d) and the initial slope (α) were strongly related to algal morphology with generally higher values for thinner species. The compensation irradiance (E_c) and saturating irradiance (E_k) were strongly related to water depth with lower values at higher depth. One advantage of thin sheet-like and filamentous species is the capability of fast growth, which is coupled to high photosynthetic rates per unit biomass (Littler et al. 1983; Falkowski and Raven 1997), resembling rather the conditions in shallow waters. In several macroalgae the photosynthetic parameters P_max and α are highly dependent on thallus morphology with higher and faster O_2 production rates for thinner and filamentous species, and lower rates for coarser and thicker species when normalized to biomass (measured as dry weight) and opposite when normalized to algal surface area (Johansson and Snoeijs 2002). Similar relationships were described for five green-algal species by Arnold and Murray (1980) as well as by Littler (1980) for 45 species of marine macroalgae from field incubations. Thus, deeper growing algal species are expected to have lower E_c and

E_k as species growing higher up in the littoral. Also, within species E_c can decrease as an acclimation to ambient light with water depth (Gómez et al. 1997).

The ideal strategy for life in deep water is represented by crustose coralline algae. They are well protected against grazing and can survive in spite of slow growth. Their thallus structure represents a horizontal light receiver with none self-shading by a single cell layer which enhances light absorption (Lüning 1990). In dependence to the clarity of water and the annual sum of photosynthetic active radiation impinging at the water surface, the lower depth limit of crustose coralline algae shifts with lower latitude from several meters in cold temperate waters (e.g., 15 m on Helgoland) to several hundred meters in tropical waters (e.g., 268 m Bahamas, Lüning 1990). The annual sum of impinging irradiance must support at least the annual need of energy for maintenance metabolism, measured by the maintenance respiration rate, and guarantee a minimum of energy surplus for establishment of growth and reproduction. Compared to cold-temperate regions, Caribbean algae are able to survive in such extreme depths due to the higher solar irradiance, a 12 hour period of day light and the clear water conditions (Jerlov type I) enables these Caribbean algae to survive in such extreme depths. For algae with a more complex, even erected thallus and the presence of nonphotosynthetic tissue as typically found in kelps, the need for light energy increases and the algae have to grow in more shallow waters as the amount of respiration and self-shading areas increases.

An ideal marker for macroalgal depth distribution seems to be the respective stable carbon isotope composition. Rapid carbon assimilation under high photon fluence rates leads to 13 C enrichments, probably due to extracellular and/or intracellular isotopic disequilibria resulting in a trend toward more positive carbon isotope values with increasing photon fluence rates (Wiencke and Fischer 1990). The pattern of isotope composition of algae grown at different depth was found in sediment trap samples from the 2,000-m deep King George Basin off the Antarctic Peninsula. It also revealed a strong contribution of seaweeds to the total organic carbon pool of the deeper basin waters in spring and summer (Fischer and Wiencke 1992).

In conclusion, distribution of marine macrophytes to the lower light limit which accommodates biomass production depends mainly on the minimal energy input (Kirst and Wiencke 1995). This is dependent on the annual fluence or minimum light level occurring in the respective depth for the maintenance of existing plant material and a surplus for growth and reproduction. Due to seasonal changes, algae in low light habitats have to live for long periods each year at photon fluence rates which do not cover their energy needs. Then, the photosynthetic activity in high light periods of the year (e.g., summer season) needs to be high enough to produce sufficient resources to endure periods with light conditions generally below the compensation point (E_c). Light saturation of growth in seaweeds is fortunately lower than those for photosynthesis (Lüning 1990) so that algae can produce enough reserve materials under favorable light conditions. Changes in the water transparency may shift the lower light limit so that the algal distribution pattern could be affected by anthropogenic changes of the light transmittance of the water body.

1.3 Photosynthesis Under Excessive Light Conditions

In contrast to the conditions at the lower algal distribution limit, photosynthetic organisms close to the water surface are exposed to high irradiances which may even exceed their light energy requirement for photosynthetically provided anabolism. Generally, these photosynthetic organisms do not suffer from energy shortage, but instead they have to invest in proteins and cellular components which protect them from potential damage by excess supply of energy (Wilhelm and Selmar 2011). As consequence a reduction of photosynthetic activity, called photoinhibition, may occur (Powles 1984; Krause 1988; Krause and Weis 1991). As defined by Franklin et al. (2003) photoinhibition is a generic outcome of the failure of photoprotection to mitigate photoinactivation. This may result under high light conditions in which damage of reaction center proteins exceeds photorepair in the complex molecular structure of photosystem II (PSII). Photoacclimation is the adjustment in structure and function of the photosynthetic apparatus that avoid or rapidly repair damage and thus mitigate (chronic) photoinhibition. Photoprotection (also called dynamic photoinhibition) refers to processes that decrease excitation transfer to the reaction centers; these processes are mainly operative in the antenna complexes. Loss of PS II reaction center function is called photoinactivation (formerly called chronic photoinhibition), often accompanied by loss of reaction center protein D_1, which can be repaired under dim light conditions. Under excessive light conditions a significant degradation of the reaction center protein (D_1) of PS II was found (Ohad et al. 1984; Mattoo et al. 1984). Nonfunctional photosynthetic centers are able to protect active centers against continuous damaging effects of excess absorbed light energy by harmless energy dissipation, mainly by heat dissipation (Guenther and Melis 1990; Öquist and Chow 1992; Critchley and Russell 1994). Photodamage occurs if the rate of the D_1-protein damage exceeds the rate of its repair process, leading to a breakdown of the D_1-protein pool (Aro et al. 1993). Photoprotection or dynamic photoinhibition is important for the regulation of quantum yield of photosynthesis, namely by the xanthophyll cycle in the chloroplasts of green and brown algae (Demmig-Adams and Adams 1992). Quantum yield of photosystem II (especially the in vivo fluorescence ratio F_v/F_m which represents photosynthetic efficiency after dark acclimation) is diminished reversibly by increasing thermal energy dissipation under strong light conditions. Carotenoids control this harmless dissipation of excessively absorbed light energy by, e.g., de-epoxidation of violaxanthin to zeaxanthin (Ruban et al. 2007) a process catalyzed by a thylakoid-bound deepoxidase that is activated by a low lumenal pH due to a high electron transport rate (Pfündel and Dilley 1993). Zeaxanthin may dissipate excessively absorbed light energy harmlessly as heat. The process is reversed by the epoxidation of zeaxanthin to violaxanthin in dim light (Xanthophyll-cycle). The low pH induces also protonation of the photosystem II protein, PSBS, which induces a conformational change to specific chlorophyll- and carotenoid-binding LHC proteins (Peers et al. 2009). LHC may aggregate leading to, e.g., PSBS–LHC–zeaxanthin complex in some green algae. As a consequence, the exciton transfer from exited chlorophylls to other chlorophylls is disabled and the LHCs are converted to heat dissipaters (Niyogi et al. 2005). Dissipation of excess excitation energy occurs by a charge transfer mechanism involving a carotenoid radical cation (Ahn et al. 2008) and/or by chlorophyll-to-carotenoid energy transfer (Ruban et al. 2007). The photosynthetic systems of algae share many central functions with land plants. But recently, an ancient light-harvesting protein (LHCSR) was described in *Chlamydomonas* which is involved in fast regulation of algal photosynthesis (Peers et al. 2009). LHCSRs are absent in vascular land plants, but present in a variety of photosynthetic organisms, such as diatoms that show an extremely high nonphotochemical energy-quenching capacity included in the photoprotection mechanism (Eberhard et al. 2008; Peers et al. 2009). LHCSR transcripts accumulate under environmental conditions known to induce photo-oxidative stress, including deprivation of carbon dioxide, sulfur, or iron, as well as high light (Peers et al. 2009). In algae LHCSR orthologues are missing only in Rhodophytes (and cyanobacteria), which dissipate excess light energy from phycobilisomes by a mechanism distinct from the typical, above-described, energy-dissipating mechanism (energetic fluorescence-quenching mechanism, q_E) (Wilson et al. 2006).

The short-term acclimation of plants to high irradiances and its relation to photosystem II photochemistry and fluorescence emission were reviewed in detail by Dau (1994a, b). Moreover, a general overview of photoinhibition, its molecular aspects and its mechanisms in the field are given by several articles in the book edited by Baker and Bowyer (1994), and the effects of a changing irradiance environment, especially on marine macrophyte physiology, were also reviewed (Franklin and Forster 1997; Häder and Figueroa 1997; Bischof et al. 2000a; Wiencke et al. 2007).

In the marine habitat macrophytes are exposed to considerable diurnal changes of the impinging photon fluence rates due to the position of the sun, clouding and, especially, the tides (Hanelt and Nultsch 2002). Therefore, at midday benthic marine algae, which grow normally underwater at dim light conditions, can be exposed to extremely high irradiances on sunny days during low tide in the intertidal. As a consequence, light energy is excessively absorbed by the photosynthetic apparatus and, hence, the extent of its photodamage increases. One of the damaging processes is the production of highly reactive oxygen species, which attack target molecules such as the D_1-protein, chlorophylls and unsaturated fatty acids (Asada and Takahashi 1987; see Chap. 6 by Bischof and Rautenberger). The damage to the photosystem is counteracted by a repair process that involves partial disassembly of inactive PSII, proteolytic degradation of the photodamaged reaction center protein (D_1) and cotranslational insertion of newly synthesized D_1 into PS II, also called D_1 repair cycle (Aro et al. 1993; Barber and Andersson 1992). Permanent photodamage occurs when scavenging of oxygen radicals by superoxide dismutase, hydrogen peroxidase or catalase is insufficient. Under light stress conditions, the concentration of active oxygen is increased either by higher production rates or by insufficient capacity of the oxygen-scavenging systems. The reactive oxygen species seem to induce inhibition of repair processes by suppression of the de novo synthesis of proteins and, in particular, of the D1 protein that are required for the repair of PSII (Nishiyama et al. 2006; Murata et al. 2007). In addition, H_2O_2 can inhibit CO_2 fixation by 50% because of the oxidation of the thiolmodulated enzymes of the Calvin cycle even at low concentrations (e.g., 10 mM) (Foyer and Shigeoka 2011). A charge recombination between the PSII primary electron acceptor in its semiquinone state and the oxidized chlorophyll donor lead to accumulation of excited triple chlorophylls (Eberhard et al. 2008). These triplet chlorophyll molecules can react with oxygen and generates harmful singlet oxygen, causing damage to PSII and other cell constituents. At the photosystem I acceptor side the redox potential under strong supersaturating light is high enough to reduce molecular oxygen to form O_2-superoxide radicals. Quenching of these radicals by carotenoids and ascorbate can protect the photosynthetic apparatus against such damage.

Nultsch et al. (1987) showed that, depending on the duration and the fluence rate of the excessive irradiation, a decrease in both the photosynthetic efficiency and capacity in the brown alga *Dictyota dichotoma* was caused by photoinhibition. Recovery in a subsequent dim light period was very fast so that in this species the photosynthetic efficiency recovered from inhibition of 80% already within 1 h. Moreover, the action spectrum of photoinhibition revealed that the photoinhibitory radiation was absorbed by all photosynthetic pigments, and that photosystem II is the main site of the photoinhibitory process. According to the definition by Franklin et al. (2003) this species shows a high potential for photoprotection.

Similiar results were presented with the red alga *Polyneura hilliae* (Nultsch et al. 1990). However, in contrast to *Dictyota*, the red algal species recovered very slowly after strong photoinhibition. In this red alga only a partial recovery was observed in complete darkness, and the recovery phase is clearly biphasic. A first fast phase occurs already in darkness, whereas the subsequent slow phase requires dim light. The potential for photoprotection in the red algal species was low compared to *Dictyota*. The above described kinetics indicates that apparently two different molecular mechanisms are involved in photoinhibition. The discrimination of dynamic and chronic photoinhibition recommended by Osmond (1994) is ingenious, according to photoprotection and photoinactivation. Studies of the kinetics revealed that especially during a fast light acclimation the reaction can be described combining two different processes of a slow fraction (P_{slow}) with a slow rate constant (k_{slow}) and a fast fraction (P_{fast}) with a fast rate constant (k_{fast}) at a given time (t).

1. The phase of inhibition is described by:
   $y_{\text{Inh}} = P_{\text{fast}} \bullet e^{(-k_{\text{fast}} \bullet t)} + P_{\text{slow}} \bullet e^{(-k_{\text{slow}} \bullet t)}$
   at which $F_v/F_m = P_{\text{fast}} + P_{\text{slow}}$ at $t = 0$

2. The phase of recovery is described by:
   $y_{\text{Rec}} = F_v/F_m - \left(P_{\text{fast}} \bullet e^{(-k_{\text{fast}} \bullet t)} + P_{\text{slow}} \bullet e^{(-k_{\text{slow}} \bullet t)}\right)$

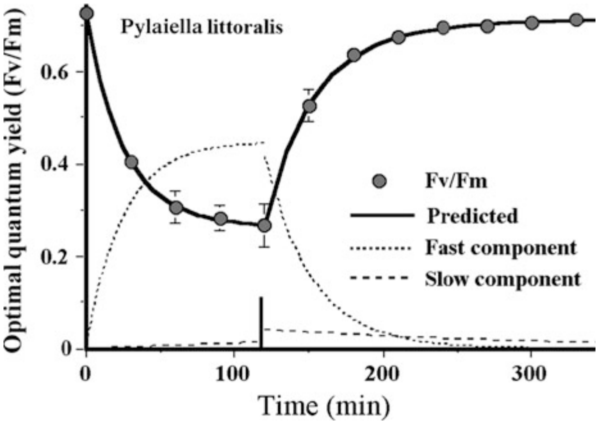

Fig. 1.1 Course of a typical optimal quantum yield curve of the brown alga *Pylaiella littoralis* during an inhibition phase of 120 min with an irradiance of 500 μmol m^{-2} s^{-1} and a subsequent period of recovery under 10 μmol m^{-2} s^{-1} white light. Points show yield measurements (F_v/F_m) dependent on the time course. The *dashed line* shows the kinetics of the slow process, the *dotted line* those of the fast process, and the *solid line* the kinetics of the predicted process combined by the slow and the fast kinetics. Mean values ± SD, $n = 3$, $r^2 = 0.999$ (after Hanelt 1998)

This explains why the course of recovery shows generally two phases (Hanelt et al. 1997a, b, c). Using these equations the data of the optimal quantum yield can be well fitted with a coefficient of determination of $r^2 \geq 0.99$ (Fig. 1.1).

In conclusion, the fast process could represent photoprotection or the activity of the xanthophyll cycle and the slow process the course of photoinactivation or the occurrence of D_1 damage and/or inactivation of reaction centers. Algae which are adapted to dim light conditions show a higher fraction of the slow process, whereas the reaction of algae adapted to strong light conditions mainly consist of the fast reaction e.g., Fig. 1.1 (Hanelt 1998).

First field experiments on photoinhibition in macroalgae were done by Huppertz et al. (1990). They showed that the midday depression of photosynthesis was clearly caused by photoprotection. Specimens of the brown alga *Fucus serratus* living in intertidal rock pools and, hence, are covered by water during low tide, showed a considerable decrease of photosynthetic activity under excessive natural light conditions. The photoinhibitory state is conserved by moderate desiccation in air in this species because the thalli show the same state of photoinhibition after reabsorbing water as measured before they became uncovered during falling tide. Thereafter it was demonstrated that the photosynthetic oxygen production measured at nonsaturating fluence rates and the optimal quantum yield (F_v/F_m) show an approximately inverse course in comparison with the fluence rate of daylight during the day (Hanelt 1992; Hanelt et al. 1993).

According to the recent review of Murchie and Niyogi (2011) the mechanisms included in photoprotection regulate absorption and dissipation of light energy. The immobility of plants does not allow leaving temporarily high light-exposed areas, but they have the ability to regulate the amount of absorbed sunlight by changes in leaf area, leaf angle, chloroplast movement and, on a molecular level, through acclimatory adjustments in LHC antenna size. Excessively absorbed light can be dissipated via several routes, including thermal dissipation. A number of other reactions within the chloroplast can act as photochemical sinks for excess electrons, and there are efficient antioxidant systems for the removal of reactive oxygen species which are produced under high energy load of the system.

1.4 Effect of Ultraviolet Radiation on Zonation of Macroalgae

In most studies on marine macrophytes, there is common sense that the sensitivity of photosynthesis to ultraviolet radiation (UVR) is a function of vertical zonation of the species (Larkum and Wood 1993; Dring et al. 1996; Bischof et al. 1998a; see Chap. 20 by Bischof and Steinhoff). Moreover, Maegawa et al. (1993) regard solar UVR as a major factor controlling the upper zonation limit of red macroalgae on the shore. The potential of UV to inhibit photosynthesis of algae was first demonstrated by Jones and Kok (1966). Results of Larkum and Wood (1993) indicated that increasing UV levels of the solar radiation can cause similar effects comparable to high PAR in all types of aquatic plants. In the field, high irradiances of PAR are generally accompanied by higher UV-radiation. The mechanisms are, however, likely to be different. UV radiation cannot be regarded as an “excessive energy input” in a proper sense. Its maximal irradiance is much smaller than that of PAR, and the UV wavebands do not contribute significant energy supply for photosynthetic chemistry. UV exhibits adverse effects on photosynthesis in a more direct way, such as its waveband with high energy content is absorbed by aromatic and sulfhydryl-containing biomolecules, causing a direct molecular damage (Vass 1997). The UV-B inhibition spectrum corresponds much more with the spectral absorption by DNA and proteins than with photosynthetic pigments or the action spectrum of photoinhibition (Jones and Kok 1966; Setlow 1974; Nultsch et al. 1987; Hanelt et al. 1992). Numerous studies have shown that recovery from photoinhibition is delayed after exposure to additional UV-B irradiation (see the review of Häder and Figueroa 1997). In contrast, Flores-Moya et al. (1999) demonstrated that in the marine macroalga *Dictyota dichotoma* a delay of recovery of photoinhibition is observed if the natural UV-B wavelength range is removed from the solar spectrum, in specimens collected from a high UV environment. This was later confirmed under simulated sunlight conditions with different aquatic plants in New Zealand (Hanelt et al. 2006) or in field studies with natural sun radiation (Hanelt and Roleda 2009). Positive effects of UV-B on growth and abundance in phytoplankton are also reported by Thomson et al. (2008); some taxa were most abundant in treatments of intermediate fluxes of UV-B radiation. This suggests that moderate UV-B irradiances may enhance protection from PAR and/or UV-A. In *Synechocystis*, UV-B radiation accompanied by low intensity visible light enhanced synergistically protein-repair capacity, which provides

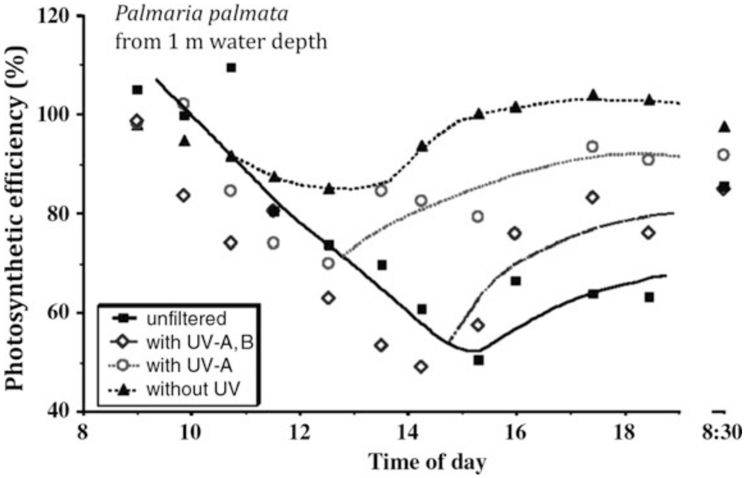

Fig. 1.2 Photosynthetic efficiency of the red alga *Palmaria palmata* during the course of the day. The day was cloudy and the fluence rate decreased continuously after 14:10 h. The photosynthetic efficiencies of the nonphotoinhibited controls, collected the day before from a depth of 1 m, were measured by the fluorescence ratio F_v/F_m and standardized to 100%. The *solid fitted line* indicates the inhibition caused by unfiltered sun radiation. The *broken* and the *dotted lines* represent the inhibition caused by radiation depleted of different UV wavelength ranges. Next morning (8:30), photosynthesis was measured again (after Hanelt et al. 1997a)

protection against photodamage (Sicora et al. 2003). Generally, field experiments at latitudes with a low UV environment (e.g., polar region) do never show UV-B repair effects in macroalgae (Hanelt et al. 1997a, b, c; Bischof et al. 2000b). This indicates a special adaptation of organisms to UV-B when they live in an environment with high solar radiation under high UV pressure. However, algae growing in deeper, UV-protected locations on the shore are more sensitive to the natural UVR as for instance the red alga *Palmaria palmata* (Hanelt et al. 1997a). This species shows a reaction which is clearly dependent on the different UVR ranges. By cutting off successively the shorter wavelengths ranges, the degree of photoinhibition decreases and recovery commences earlier during the course of the day (Fig. 1.2).

Various factors contribute to the individual sensitivity of algae toward solar radiation, e.g., growth depth (Sagert et al. 1997; Dring et al. 1996; Bischof et al. 1998b), season (Gómez et al. 1995a), position within and below the canopy (Stengel and Dring 1998), life history stage as well as the different parts and sizes of the thalli (Gómez et al. 1995b; Dring et al. 1996; Hanelt et al. 1997b; Karsten and Wiencke 1999). Thus, acclimation to the ambient radiation plays an important role in photosynthesis of marine macroalgae. A study on three abundant brown algal species from Spitsbergen (*Saccharina latissima, Alaria esculenta,* and *Saccorhiza dermatodea*) shows that individual photosynthetic performance reflects changing light climate in accordance with depth (Bischof et al. 1998b). Photosynthetic acclimation was found for both ambient PAR and UVR. Exposure to artificial UVR reduces photosynthetic rates in deep water plants significantly while photosynthesis in the same species collected from shallow waters is unaffected. To cope with higher irradiance levels in shallow waters a capability for fast recovery from light stress is one prerequisite (Hanelt 1998).

The acclimation potential of maximal quantum yield of photosynthesis to changing radiation conditions was studied in detail in the Arctic/cold temperate brown alga *Alaria esculenta* (Bischof et al. 1999). In this species, acclimation to changing radiation conditions occurs within very few days. This is of great ecological importance as algae, subjected to 6 months of darkness during the Arctic winter and sea ice with snow cover shielding the algae from solar radiation in spring, become suddenly exposed to high radiation, and thus also to UV, as soon as sea ice breaks up. *A. esculenta* shows two different responses involved in the acclimation of maximal quantum yield of photosynthesis. At first, after a few days of exposure to artificial UVR, the recovery from induced photoinhibitory processes proceeds significantly faster; later, the degree of photoinhibition decreases. This implies again that different molecular mechanisms are involved in photoacclimation. In conclusion, photosynthesis of macroalgae from the intertidal zone is rather resistant to natural UV-B radiation. Algae from the upper sublittoral seem to be able to acclimate rapidly to fast changes of solar irradiance, consequently reducing the adverse effects of UVR exposure or even need UV-B as induction for repair processes (Hanelt and Roleda 2009). Deep water algae react highly sensitive to UVR (Bischof et al. 2000b), but, due to the absorption of the water body, UV-B is no natural component of the ambient light at higher depths. However, it is important to note that UVR may also exert adverse effects on the algae, e.g., growth rate reduction and/or reproductive success which is not reflected by a reduced photosynthetic activity.

Two aspects have received little attention so far. In many Polar species growth rates are highest in Spring (Wiencke 1990a, b; see also Chap. 13 by Wiencke and Amsler), which are also affected by UVR, and not only photosynthesis of young thallus parts (Dring et al. 1996; Wood 1987*)*. Moreover, some species from the Arctic partly reproduce in spring. During this time, algal spores were found to be the most light-sensitive life history stage of the studied brown algae and are strongly affected by increased UV-B radiation, both in respect to their photosynthetic performance and their susceptibility to DNA damage (Wiencke et al. 2000). As has been widely publicized, increased UV-B due to ozone depletion occurs mainly in the Polar Spring due to atmospherical and geographical reasons. Therefore, Polar species will be most exposed to the anthropogenic increase of UV-B radiation.

1.5 Light Absorption and Light Spectrum

The color of the algae is mainly based on the accessory photosynthetic pigments of the LHC. Engulfment of a cyanobacterium or eukaryotic microalga by a process called endosymbiosis is a cause of physiological, structural and genetic adaptation of the different types of chloroplasts in evolution. The brown color typical for the

Phaeophyceae is caused by light absorption of the carotenoid fucoxanthin, and the red color of the Rhodophyceae by the phycobiliproteins. If the LHC consists mainly of chlorophylls, the color is green, as is typical for the Chlorophyceae. The different absorption characteristics of the respective LHC correspond to different underwater light spectra. Different light qualities occur within the water body by absorption and scattering of light (Jerlov 1976) especially with increasing water depth and/or turbidity. Generally, the blue-green waveband penetrates deepest into the water body as the shorter and longer wavelength are more absorbed by the water molecules or scattered by particles. Photosynthetic apparatus of algae has adapted to these different wavebands. The occurrence of the various types of pigments in the LHC and their arrangement in both photosystems are responsible for different photosynthetic efficiencies of different spectral wavebands which affect photosynthetic activity. The action spectrum of photosynthesis of red algae shows a so-called blue and red drop, first described by Haxo and Blinks (1950). Green light is best absorbed by the phycobilines so it shows the highest photosynthetic rates in red algae. In contrast blue and red/far red light does not induce high electron transport rates because chlorophyll molecules act as the main antenna pigment in photosystem I so that the reaction center of PS I is primarily activated (Butler 1978). Blue and far red light induces principally charge separation in the reaction center of PS I and cyclic electron transport around PS I. As charge separation of PS II in red algae is not induced to an equal amount, linear electron transport rate is small and oxygen production rate is low (Haxo and Blinks 1950; Hanelt et al. 1992).

Engelmann (1883, 1884) pointed to the fact that most green algal species occur in the eulittoral and upper sublittoral, whereas brown algae grow often in deeper zones and many red algae can be characterized as deep water species. In deep water, where blue-green light prevails, the red pigments of the Rhodophyceae allow an efficient absorption (Biebl 1962). However, this is only partly valid because the absorption characteristic depends also on several other factors, especially the thallus morphology. It applies more to coastal waters than to oceanic waters (Larkum et al. 1967). If the algal thallus is thick enough it appears nearly black and absorbs light over the whole spectral range, as typical for brown kelps (Lüning 1990). In addition accessory pigments do enhance light absorption in the blue-green range and examples of green algae growing in deep waters are not rare (Dring 1981, 1982; Ramus 1981). Anyhow, the deepest algae found are crustose red algae with a quite low light demand (Littler et al. 1986), which is not only due to their low growth rate and special morphology (one absorption layer) but also due to their capability to use the impinging photons very efficiently in the blue-green wavelength range (Hanelt et al. 2003). In vivo absorptance of thin and thick algal thalli of the different pigment groups was investigated by Lüning and Dring (1985). Their study demonstrated that a good correlation exists between spectral thallus absorption and action spectrum of photosynthesis, as well as a greater thallus thickness supports photosynthetic activity also when wavebands are slightly absorbed. Leukart and Lüning (1994) demonstrated in several red algal species that growth rate and photosynthesis depends on the light quality during culture and on the pigment content under these conditions. The light requirements were lowest in green light for all red algae investigated. The action spectra of growth followed the photosynthetic action spectra, with maximum efficiencies in the green wavebands, corresponding to the wavelength distribution occurring in deep coastal waters. This points to the importance of light quality for survival at low photon fluence rates and corroborates the findings of Harder and Bederke (1957), Beer and Levy (1983) and Glover et al. (1986, 1987).

1.6 Light as an Environmental Signal

The color of light can induce photomorphogenetic effects, enzyme activity induction or controls the life cycle of the algae. Light is not only the primary energy source but it also provides them with information to modulate developmental processes such as phototaxis of swarmers, phototrophic reactions, chloroplast movement, shade avoidance, circadian rhythms, etc. (Lüning 1990; Kleine et al. 2007). Plants can detect almost all facets of light, including direction, duration and wavelength using three major classes of photoreceptors: the red/far-red light-absorbing phytochromes which are only proven to be a sensor in green algae (Dring 1988; Rüdiger and López-Figueroa 1992), the blue/UV-A light-absorbing cryptochromes and phototropins, and UV-B-sensing UV-B receptors (Chen et al. 2004). A phytochrome-like protein was described in all pigment groups of the macroalgae; however, red/far-red forms were isolated only from green algae (López-Figueroa et al. 1989, 1990). Cryptochromes seem to be widespread in the group of Phaeophyta and, possibly, among chromophyte algae in general (Dring 1988). The photoreceptors perceive light signals and initiate intracellular signaling pathways involving proteolytic degradation of signaling components and large reorganization of the transcriptional program to modulate plant growth and development (Chen et al. 2004). Nitrate reductase activity in green algae and biliprotein accumulation in some red algae may be stimulated by blue or green light, and an interaction with phytochrome like photoreceptors was indicated (López-Figueroa and Rüdiger 1991; López-Figueroa and Niell 1991). Blue light, similar to low light, induces an increase in the number of pigment systems per electron transfer chain in green algae, whereas red light blocks chlorophyll b synthesis and leads to a decreased light-harvesting system together with an increase in the number of reaction centers per electron transfer chain (Senger et al. 2002). The latter equates an adaptation to strong light conditions. The opposite behavior of algae and higher plants to red or blue light corresponds to the different spectral conditions in their habitat. In deep water regions algae grow under blue light conditions whereas higher plants are exposed to a higher fraction of red light. However, Senger et al. (2002) come to the conclusion that the phylogenetic relationship is the major factor for this difference in the light adaptation between algae and higher plants rather than a long-term adaptation to the environment.

The phototactic response of swarmers of the brown algae *Scytosiphon lomentaria* and *Petalonia fascia* causes a photoaccumulation at a peak of 450 nm, and no effect was found at a wavelength above 550 nm, as it is typical in a blue light response (Flores-Moya et al. 2002). In *Ectocarpus siliculosus* the waveband between 430 and 450 nm was found to be the most effective for photoaccumulation of the male gametes (Müller et al. 1987), also shown by the action spectrum of their phototactic response (Kawai et al. 1990). The action spectrum of the chloroplast movement of the brown alga *Dictyota dichotoma* resembles the absorption spectrum of the blue light photoreceptor cryptochrom and serves as a control of the light absorptance in brown seaweeds (Hanelt and Nultsch 1989). In addition a blue light receptor is also responsible for the egg release in *D. dichotoma* (Lüning 1990). Phototrophic reactions have been observed, e.g., in the zygotes of *Fucales*, haptera of *Laminariales* or rhizoids of kelps, and even more examples on light control are given in the seaweed book of Lüning (1990).

Circadian and circannual rhythms in algae are also controlled by light that time metabolic, physiological and/or behavioral events to occur at optimal phases of the daily or annual cycle. Eukaryotic algae serve for long time as model system to study circadian rhythms. (Suzuki and Johnson 2001). For example, UV shows the strongest effect of destruction at sunset and the early night when UV levels are naturally low and, hence, the control due to the daily clock enhances the fitness during the day at higher UV levels (Nikaido and Johnson 2000). Photoperiodic time measurements, i.e., the detection of the lengths of day or night, is the ability to sense the season of the year and to respond appropriately so as to adapt to seasonal changes in the environment (Lüning and tom Dieck 1989). The red Antarctic alga *Palmaria decipiens* shows a seasonal pattern of photosynthetic activity and pigment synthesis (Lüder et al. 2001; see also Chap. 13 Wiencke and Amsler). Maximal electron transport rates of photosynthesis and pigment content increased in *P. decipiens* during mid-autumn and winter. Highest photosynthetic capacity and size and number of phycobilisomes were observed in spring according to sea ice break up so that photosynthetic performance was most effective during clear water conditions. In summer the photosynthetic apparatus degrades and the life strategy of the algae was defined as season anticipator (Lüder et al. 2001). This is contrary to species (e.g., *Iridaea cordata* or *Adenocystis utricularis*) where photosynthesis and growth follow the seasonally increasing daylight period and are defined as season responders with opportunistic life strategy. After an artificially prolonged dark period of 6 months *P. decipiens* lost its ability to photosynthesize with degradation of its light harvesting antennae, the phycobilisomes, and probably through degradation of the reaction centers of photosystem II. Re-illumination within 1 day induced fast accumulation of chlorophyll a and enables active photosynthesis, which indicates rapid repair mechanisms (Lüder et al. 2002). This shows how light controls the activity of the photosynthetic apparatus. The formation of erect thalli in red and brown algae, from a prostrate system (a crust or branching filaments), is commonly controlled by the photoperiod, and either gametogenesis or sporogenesis may also occur in response to changes in daylength (Dring 1988). In spring the erect siphonous thallus of *Scytosiphon* and the folios thalli of the green *Monostroma* appear in the cold temperate eulittoral zone, whereas they survive the summer to winter month as crustaceous or respective *Codiolum* phase

(Lüning 1990). Short-day responses of *Laminaria hyperborea* and *Constantinea subulifera* result in the initiation of a new blade in the autumn or winter while the rate of growth of the young blades of a kelp species (*Pleurophycus gardneri*) is stimulated by long-day conditions (Dring 1988). In contrast, photoperiodism in unicellular algae is unknown and seasonal behavior shall be governed by ecological factors, such as temperature, irradiance and nutrient levels (Lüning 1990).

1.7 Conclusive Remarks

Distribution of marine macrophytes in deep water with low light depends mainly on the minimal energy input. The annual fluence or minimum light level occurring in the respective depth for maintenance of existing plant material must have a surplus for growth and reproduction. During winter seasons algae in low light habitats have to live for long periods each year at photon fluence rates which do not cover their energy needs so that the energy must be chemically stored in the bright light seasons. As light saturation of growth is fortunately lower than those for photosynthesis, deep water algae can still produce enough reserve materials under favorable light conditions. In contrast, at the water surface, irradiance can be too high and the algae have to avoid photodamage by additional investment in proteins and cellular components for protection. These algae exhibit strong and fast regulation of photosynthesis and perform photoprotective mechanisms, i.e., harmless heat dissipation.

However, light does not only serve as a source for energy in photoautotrophic organisms, but is also an environmental signal for regulation and development, inducing changes in photoperiodism (dependence on daylength), photomorphogenesis (dependence on spectral range) and phototropism. In these cases the signal character of light is evident from the low light requirement to induce a reaction. Special photoreceptors are the sensors in the signal chain, whereas the energy to perform the respective reaction is mostly provided by photosynthesis and thus channeled from the energy absorbed by photosynthetic pigments. The variety of the sensors and their responses in algae seem to be more varied than those among flowering plants.

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