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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

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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 $\geq$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 $F_{\text{v}}/F_{\text{m}} = P_{\text{fast}} + P_{\text{slow}}$ at $t = 0$

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

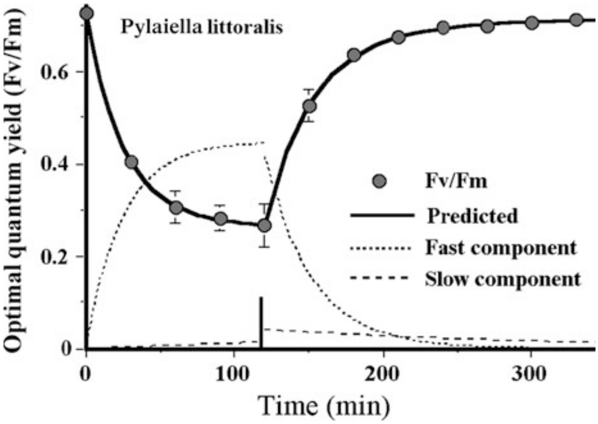

Fig. 1.1 Course of a typical optimal quantum yield curve of the brown alga *Pylaiella littoralis* during an inhibition phase of 120 min with an irradiance of 500 µmol m^{-2} s^{-1} and a subsequent period of recovery under 10 µmol m^{-2} s^{-1} white light. Points show yield measurements (F_v/F_m) dependent 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

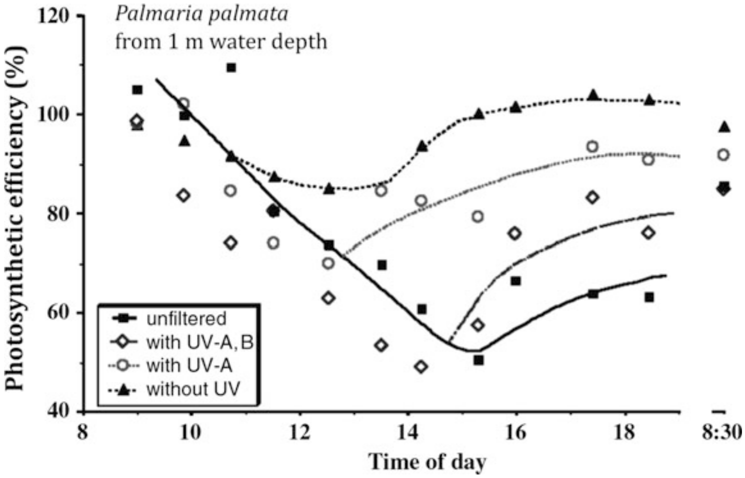

Fig. 1.2 Photosynthetic efficiency of the red alga *Palmaria palmata* during the course of the day. The day was cloudy and the fluence rate decreased continuously after 14:10 h. The photosynthetic efficiencies of the nonphotoinhibited controls, collected the day before from a depth of 1 m, were measured 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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Chapter 2
Morpho-functionality of Carbon Metabolism in Seaweeds

Iván Gómez and Pirjo Huovinen

2.1 Introduction

The process by which inorganic carbon is converted into organic forms driven by the solar energy is unique to photoautotrophic organisms (some types of prokaryotes, cyanobacteria, eukaryotic algae, and plants). Although in many cases the underlying mechanisms and enzymatic machinery associated with carbon metabolism are essentially similar to those found in higher plants, seaweeds show some differences, especially related with carbon acquisition and concentration, biochemical strategies to avoid the oxygen/CO_2 interference of RUBISCO (photorespiration), and C4 metabolism. Other striking characteristic lies in the remarkable versatility of the different biochemical pathways and products that allow seaweeds to operate under resource limitation (e.g., CO_2, light, nutrients) and under changing environments. On the other hand, seaweeds exhibit a great variety of storage carbohydrates (e.g., mannitol, floridoside). These compounds can be remobilized during growth and reproduction, and are also normally involved in a series of reactions associated with osmoregulation and antioxidant activity (see Lobban and Harrison 2000 for an overview).

Seaweeds are multicellular, macroscopic organisms and thus a major aspect of carbon metabolism that makes them different from other groups of algae and cyanobacteria is its dependency on gross morphology. The morpho-functional processes of carbon assimilation occurring in foliose and finely branched seaweeds can be considerably different from those of, e.g., coarsely branched and leathery species (Ramus 1978; Rosenberg et al. 1995). In many large brown algae, seasonal decoupling of carbon assimilation and anabolic processes, long-distance transport of photoassimilates, and biomass formation restricted to meristematic cells are

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conceived as fundamental adaptations for optimal allocation of energy in changing environments (Gómez et al. 2007).

In terms of its ecological importance, the photosynthetic transformation of inorganic carbon into organic molecules carried out by benthic seaweeds accounts for an important fraction of the coastal primary production and biomass. Furthermore, the fate of seaweed-derived organic material is central for the higher trophic levels and geochemical processes of the coastal ecosystems (Mann 1973).

2.2 Inorganic Carbon Acquisition

Seaweeds must use CO_2 dissolved in seawater as inorganic carbon source. In the surface water the different species of inorganic carbon (CO_2, HCO_3^-, and CO_3^{2-}) are in equilibrium in the so-called carbonate buffer system (see also Chap. 19 by Roleda and Hurd). For example, at partial pressure of 365 μatm, pH 8.1, 25°C, and salinity of 35 psu, the CO_2 concentration is close to 10.4 μmol kg^{-1}, while HCO_3^- and CO_3^{2-} have values of 1,818 and 272 μmol kg^{-1}, respectively. Thus, only a small fraction (~0.5%) is in the form of CO_2 (Zeebe and Wolf-Gladrow 2001). Diffusion of CO_2 in water (0.16×10^{-4} cm^{-2} s^{-1}) is four orders of magnitude lower than in air (0.16 cm^{-2} s^{-1}), which has important consequences for photosynthesis (Badger and Spalding 2000). In the case of aquatic organisms, the entry of CO_2 into the cell is normally limited by the diffusion boundary layer, whose thickness, and hence its resistance, depends on the form and volume of the alga as well as the speed of the water flow around it. For example, for an aqueous phase system with a diffusion coefficient of 1.5×10^{-5} m^{-2} s^{-1} and a boundary layer of 15 μm, a maximum flux of CO_2 close to 2.6 m^{-2} s^{-1} can be estimated (Falkowski and Raven 1997). Due to these constraints the sole diffusive entry of CO_2 does not support photosynthetic demands and thus algae can suffer carbon limitation. This situation has been documented for some subtidal red algae that apparently rely on CO_2 diffusion as the only mechanism of inorganic carbon uptake (Raven and Beardall 1981; Maberly 1990). The majority of seaweeds, however, have developed the capacity to concentrate CO_2 in order to guarantee an adequate supply to RUBISCO. One of the most efficient carbon concentrating mechanism (CCM) is the active transport not only of CO_2 but also HCO_3^-, which accounts for up to 95% of the total dissolved inorganic carbon in seawater (reviewed by Raven 2010; see also Chap. 4 by Gordillo). In many cases, the HCO_3^- is an intermediate pool, which is converted to CO_2 in the vicinity of RUBISCO (Badger and Price 1994). Similar to strict CO_2 users, there is depth dependence in the ability of seaweeds to use HCO_3^- with a tendency of higher affinity for HCO_3^- in seaweeds occupying the upper littoral zones compared to their counterparts from deeper locations (Sand-Jensen and Gordon 1984; Mercado et al. 1998; Murru and Sandgren 2004).

The principal way by which algae utilize HCO_3^- is through the enzyme carbonic anhydrase (CA). This enzyme catalyzes the interconversion between HCO_3^- and CO_2 in distinct sites outside or inside the cell (Badger and Price 1994; Badger 2003) and its activity has experimentally been demonstrated in different seaweeds (Haglund et al. 1992; Mercado and Niell 1999). CA activities can vary considerably depending on various environmental factors (e.g., temperature, UV radiation) and at different temporal scales (Flores-Moya et al. 1998; Gómez et al. 1998a, b; Choo et al. 2005). Various surveys carried out in North Atlantic (Giordano and Maberly 1989), Mediterranean (Mercado et al. 1998, 2009), southern Chile (Huovinen et al. 2007), and the Arctic (Gordillo et al. 2006) have confirmed that the CA-based inorganic carbon acquisition is broadly extended in seaweeds, suggesting that this metabolic ability is advantageous in coping with changes in the availability of ambient CO_2. Other mechanisms include the nondiffusive incorporation of HCO_3^- via a specific transporter or proton pump, e.g., ATPase, an OH^-/HCO_3^- antiport system, which have been reported, e.g., in the brown alga *Laminaria digitata* (Klenell et al. 2002), and the green alga *Cladophora* (Choo et al. 2005), or an anion exchanger at the plasmalemma as has been postulated for *Ulva* sp. (Drechsler et al. 1994). Many aspects dealing with the nature of the transporter or the unbalance in the electrochemical potential across membranes remain unknown, but apparently its operation does not preclude the action of any intracellular CA (Raven and Lucas 1985).

Unlike terrestrial C3 plants that base their inorganic acquisition on diffusive CO_2 entry, the majority of seaweeds exhibit functional CCMs (Raven 2010). For example, the model of carbon acquisition/assimilation in the Chlorophyta *Ulva* sp. is based on the capacity of this alga to convert HCO_3^- into CO_2 via external CA and also to transport actively HCO_3^- through the plasmalemma (Beer 1996). If one considers that at normal atmospheric CO_2 level (350 ppm, chloroplast flux of CO_2 of about 2.8 mM s^{-1}), the uncatalyzed rate of interconversion of CO_2 to HCO_3^- is 10,000 times slower than the biological flux via CO_2 fixation by RUBISCO, then the action of CA is necessary in seaweeds (Badger and Price 1994). In the case of some intertidal algae such as *Fucus*, CCMs have also been proposed to serve as an inhibitor of the oxygenase activity of RUBISCO (photorespiration) during emersion periods (Kawamitsu and Boyer 1999) (see below). Overall, the ecological significance of these mechanisms in seaweeds, as well as their prevalence in relation to phylogeny and biogeography, has been proposed (Surif and Raven 1990; Raven 1991; Mercado et al. 2009). An increasingly relevant issue is the unpredictable effect of present and future global change-driven increases in CO_2 concentration, which probably have impact on carbon acquisition patterns of seaweeds (Raven et al. 2002; Hurd 2000; Mercado et al. 2009, see Chap. 19 by Roleda and Hurd).

2.3 Photosynthetic Carbon Fixation

2.3.1 Calvin–Benson Cycle and RUBISCO

The process of fixation of CO_2 into ribulose 1,5-bisphosphate (RuBP) to form triose phosphate is denominated photosynthetic carbon reduction cycle or Calvin–Benson cycle and occurs in the chloroplasts of seaweeds. The whole cycle consists of three major reactions: carboxylation, reduction, and regeneration. The carboxylation part can be summarized as:

3 Ribulose-1,5-bisphosphate (RuBP) + $3CO_2$ + H_2O + 2 × 3 Phosphoglycerate (PGA)

The chloroplast enzyme ribulose1,5 bis-phosphate carboxylase/oxygenase (RUBISCO) is central in the carboxylation phase. The enzyme has a complex structure and is formed by eight large catalytic subunits of approximately 53 kDa encoded in the chloroplast genome and eight small 15 kDa mass peptides encoded in the nucleus. Different types of RUBISCO (I, II, III, and IV), which vary in different groups of photosynthetic organisms according to their kinetic characteristics, have been recognized (Tabita et al. 2008). Only variants of the type I have been found in seaweeds (Raven 1997). Although the enzyme is dispersed in the chloroplast stroma, a portion of the RUBISCO is located in proteinaceous bodies denominated pyrenoids, which are present in many seaweed groups (McKay et al. 1991). The role of pyrenoids in carbon metabolism is still not well understood; however, the evidence that other enzymes (e.g., RUBISCO activases) are also located in these bodies suggests its functional involvement in carbon fixation in the chloroplast.

The Calvin–Benson cycle is autocatalytic, i.e., its reactions generate the biochemical intermediates, which enhance the rate of carbon fixation in the case of increase in its concentration. It has been demonstrated that thallus regions of seaweeds with higher relative abundances in RUBISCO exhibit the highest rates of carbon fixation (Cabello-Pasini and Alberte 2001b). On the other hand, activity of RUBISCO is highly dependent on the environmental factors (Raven 1997; Bischof et al. 2002). During the photosynthetic carboxylation, CO_2 is incorporated into the carboxyl group of the RuBP to form an unstable intermediate (enediol) and finally 3-phosphoglycerate (PGA), which is the first and most important compound of the cycle that is labeled in presence of ^{14}C (Calvin 1956; Beer and Israel 1986). In the reduction phase, the main reaction is the conversion of PGA in glyceraldehyde 3-phosphate (GAP) through the use of ATP and NADPH formed in the photochemical reactions by GAP-dehydrogenase (GAP-DH). Due to this dependence, a feedback between both processes has been examined in some seaweeds, mainly in relation with environmental factors that affect thylakoid membranes (Bischof et al. 2002). The third stage of the carbon fixation process is the regeneration that allows maintaining the operation of the cycle through the constant supply of RuBP from molecules of triose phosphate. In the ATP-consuming process, which includes isomerization, condensation, hydrolization, and phosphorylation reactions, three molecules of RuBP are formed from five molecules of triose phosphate (Nelson and Cox 2004).

2.3.2 Rates of Carbon Fixation

Rates of RUBISCO-catalyzed carbon fixation measured using radioactive carbon isotopes ($H^{14}CO_3$) vary in seaweeds depending on different environmental and endogenous factors. Values compiled in Table 2.1 indicate that, irrespective of taxa

Table 2.1 Summary of photosynthetic carbon fixation and light-independent carbon fixation (LICF) rates as well as percentage ratios of selected seaweeds from three major taxonomic divisions and biogeographic regions

Species	Location	Thallus part	Light ^{14}C fixation (µmol ^{14}C h^{-1}) g^{-1} FW	LICF	Ratio (%)	References
Chlorophyta						
Cladophora columbina	Pacific Grove, California	Whole thallus	6.6	0.06	0.90	Cabello-Pasini and Alberte (1997)
Codium fragile	Helgoland Island, North Sea	Whole thallus	20.5	0.27	1.31	Kremer (1981)
Codium decorticatum[a]	Atlantic coast of Florida	Whole thallus	20.6	0.1	0.48	Reiskind et al. (1988)
Ulva lactuca	Pacific Grove, California	Whole thallus	27	0.18	0.66	Cabello-Pasini and Alberte (1997)
Ulva lactuca[b]	Helgoland Island, North Sea	Whole thallus	14.6	0.08	0.55	Kremer (1981)
Udotea flabellum	Florida, Gulf of Mexico	Blades	10.1	0.65	6.22	Reiskind et al. (1988)
Rhodophyta						
Delesseria sanguinea[c]	Helgoland Island, North Sea	Whole thallus	7.95	0.06	0.75	Kremer (1981)
Chondracantus canaliculatus	Pacific Grove, California	Whole thallus	15.6	0.07	0.45	Cabello-Pasini and Alberte (1997)
Chondrus crispus	Helgoland Island, North Sea	Whole thallus	4.2	0.18	0.75	Kremer (1981)
Gracilaria lemaneiformis	Pacific Grove, California	Apical branch	12	0.06	0.50	Cabello-Pasini and Alberte (1997)
Iridaea cordata	Pacific Grove, California	Whole thallus	14.4	0.07	0.48	Cabello-Pasini and Alberte (2001a)
Iridaea cordata[d]	King George I., Antarctica (culture)	Whole thallus	2.5–15	0.2–2.1	1.9–17.2	Weykam (1996)
Palmaria decipiens	King George I., Antarctica (culture)	Young blade	11.6	0.20	1.72	Thomas and Wiencke (1991)
Palmaria decipiens[d]	King George I., Antarctica (culture)	Whole thallus	4–13	0.12–1.59	0.7–31.1	Weykam (1996)
Plocamium cartilagineum	Pacific Grove, California	Apical branch	12	0.04	0.33	Cabello-Pasini and Alberte (1997)
Phaeophyceae						
Ascophyllum nodosum	Tay Estuary, East Coast of Scotland	Blades	15	0.37	2.46	Johnston and Raven (1986)
Ascoseira mirabilis	King George I., Antarctica (culture)	Growing zone	11.4	0.7	6.14	Thomas and Wiencke (1991)
Ascoseira mirabilis	King George I., Antarctica (culture)	Apical zone	15.8	1.5	9.50	Gómez et al. (1995a, b)
Desmarestia anceps	King George I., Antarctica (culture)	Whole thallus	29.7	1	3.36	Thomas and Wiencke (1991)
Desmarestia antarctica	King George I., Antarctica (culture)	Young thallus	43.9	1.2	2.73	Thomas and Wiencke (1991)
Egregia menziesii	Pacific Grove, California	Lateral blade	16.2	0.11	0.67	Cabello-Pasini and Alberte (1997)
Eisenia arborea[e]	Helgoland I., North Sea	Blades	18.5	0.71	3.83	Kremer (1981)
Fucus serratus	Helgoland I., North Sea	Growing zone	17.4	0.70	4	Kremer (1981)
Himantothallus grandifolius	King George I., Antarctica (culture)	Young thallus	11	0.40	3.63	Thomas and Wiencke (1991)
Laminaria setchellii	Pacific Grove, California	Growing zone	15	1.92	12.80	Cabello-Pasini and Alberte (2001b)

(continued)

Table 2.1 (continued)

Species	Location	Thallus part	Light ^{14}C fixation	LICF	Ratio (%)	References
			(μmol ^{14}C h^{-1}) g^{-1} FW			
Laminaria digitata	Helgoland I., North Sea	Blade	5	0.38	7.60	Kremer (1981)
Laminaria digitata	Helgoland I., North Sea	Growing zone	5.8	1.61	27.75	Kremer (1981)
Laminaria hyperborea	Helgoland I., North Sea	Growing zone	2.1	1.01	48.09	Kremer (1981)
Laminaria solidungula	Beauford Sea, Alaskan High Arctic	Growing zone	7.6	0.34	4.47	Dunton and Schell (1986)
Lessonia nigrescens[f]	Valdivia, South East Pacific coast	Whole thallus	5.4–47.5	2.3–9.6	20.2–42.3	Gómez et al. (2005)
Lessonia nigrescens	Valdivia, South East Pacific coast	Growing zone	21	3.8	18.09	Gómez et al. (2007)
Macrocystis pyrifera	Corona del Mar, California	Inmature blades	51.1	0.2	0.39	Arnold and Manley (1985)
Pelvetia compressa	Pacific Grove, California	Apical blade	10.3	1.10	10.67	Cabello-Pasini and Alberte (1997)
Saccharina latissima	Helgoland I., North Sea	Growing zone	5.5	0.92	16.72	Kremer (1981)
Stephanocystis osmundacea	Pacific Grove, California	Lower blade	7.2	1.14	15.8	Cabello-Pasini and Alberte (1997)

Values were compiled from studies using ^{14}C labeling. Ratio (%) represents the proportion of LICF relative to photosynthetic carbon fixation

[a] A Chl *a* content of 0.5 mg g^{-1}FW was assumed

[b] A FW:DW ratio of 0.3 was assumed

[c] A FW:DW ratio of 0.2 was assumed

[d] Range from seasonal data

[e] A FW:DW ratio of 0.18 was assumed

[f] Range between different thallus parts

or geographical region, carbon fixation reaches maxima of close to 40–50 μmol ^{14}C g^{-1} FW h^{-1}. However, age and thallus part can be relevant components of variability. For example, in complex morphs (e.g., some red algae and large brown algae) ^{14}C fixation can considerably increase in mature thallus regions (which attain a well-developed photosynthetic apparatus) compared to meristematic (growing) zones (Küppers and Kremer 1978; Gómez et al. 2007). At a molecular level, the number of active sites (~4–8 mM), the concentrations of CO_2, levels of O_2 (which competes with CO_2), and RuBP are key factors determining the in vivo kinetics of RUBISCO (Woodrow and Berry 1988). In contrast to the terrestrial C4 plants enriching the concentration of CO_2 via decarboxylation of C4-acids (van Caemmerer and Furbank 2003), seaweeds increase the availability of inorganic CO_2 to RUBISCO (and in parallel inhibits the oxygenase activity of the enzyme) through the action of CCMs (Raven 2010).

2.3.3 Photorespiration

The oxygenase property of RUBISCO, mainly of organisms with diffusive entry of CO_2, is a relevant topic in photosynthetic physiology. In fact, RUBISCO catalyzes the competitive oxidation of RuBP by fixation of O_2 to RuBP to form glycolate and PGA, a pathway-denominated C2 oxidative photosynthetic carbon cycle, which coexists with the Calvin–Benson cycle. In strict sense, the term “photorespiration” implies the consumption of O_2 and release of CO_2 in the light and thus the process depends on the CO_2/O_2 balance, the so-called CO_2 compensation. At low partial pressure of CO_2 and high O_2, photosynthetic carbon fixation is competitively inhibited by the oxygenase activity of RUBISCO with formation of CO_2 from the metabolism of glycolate (Raven et al. 2005). Thus, photorespiration is integrated in the whole photosynthetic carbon metabolism (Tolbert 1997).

Photorespiration in seaweeds has been less studied than in other photosynthetic organisms, probably because seaweeds exhibit CCMs. However, an effect of O_2 on carbon fixation has been demonstrated for some representative seaweeds, which exhibit ratios of oxygenase to carboxylase activities between 0.1 and 0.25 (Raven 1997; Giordano et al. 2005). In seaweeds physiologically resembling C3 plants, e.g., understory red algae that acquire carbon via diffusive CO_2 entry, the effects of photorespiration on photosynthetic carbon fixation are higher than in other groups (Raven 2010). In addition, the detection of various enzymes involved in the glycolate metabolism (e.g., P-glycolate phosphatase, glycolate oxidase, and glycolate dehydrogenase) (Gross 1990; Suzuki et al. 1991) as well as some of their products in different seaweeds (Reiskind et al. 1988) suggests that photorespiratory carbon oxidation is widespread in these organisms and in many ways similar to terrestrial plants (Raven 1997). The fate of glycolate in the cell, which includes its oxidation to glyoxylate in peroxisomes and further conversion to amino acids and CO_2, has been studied only in some seaweeds (Iwamoto and Ikawa 1997). Overall, although the implications of the photorespiratory pathway for seaweed ecology and its reason of maintenance along the evolution of algae are not well understood, its expression has been demonstrated and apparently, under certain environmental conditions, it can have consequences for the whole carbon metabolism of algae (Raven 1997).

2.4 Light-Independent Carbon Fixation

Carboxylation is not an exclusive feature of RUBISCO; seaweeds are equipped with a suite of diverse nonphotosynthetic enzymes that, like C4 and CAM in plants, are able to carboxylate and decarboxylate various C3 and C4 compounds. Light-independent carbon fixation (LICF) is also called "dark carbon fixation" or "β-carboxylation," since inorganic carbon is fixed into the β-site of acceptors such as phosphoenolpyruvate (PEP) or pyruvate. Two enzymes, phosphoenolpyruvate carboxylase (PEPC) and phosphoenolpyruvate carboxykinase (PEP-CK), are especially important in seaweeds. The role of PEP-CK, which uses CO_2 as inorganic carbon source, in LICF has been demonstrated for various species of seaweeds, in particular large brown algae (Küppers and Kremer 1978; Johnston and Raven 1986; Cabello-Pasini et al. 2000). In contrast to PEPC, during the PEP-CK catalysis the energy of the phosphorylated group of PEP is saved by phosphorylation of nucleoside diphosphates. The first studies using radiocarbon (^{14}C) in different groups of seaweeds revealed that amino acids such as aspartate, glutamate, citrate, and alanine were primarily ^{14}C labeled (Akagawa et al. 1972; Kremer 1981; Kerby and Evans 1983). The formation of oxalacetic acid (OAA) as a key intermediate of the Krebs cycle, suggested a link with anabolic processes (Kremer 1981). In fact, an apparent function of LICF is the replenishing of carbon via "anaplerotic" reactions, especially when pyruvate is degraded to acetyl-CoA during glycolysis (Kremer 1981). However, LICF reactions do not increase the net fixed carbon but are essential for cell metabolism, i.e., the pathway provides indispensable C4 acids that are not synthesized in the Calvin–Benson cycle.

Like photosynthetic C-fixation rates, LICF rates show considerable variation among different seaweeds; however, there is a tendency of higher values in brown algae compared to Chlorophytes and Rhodophytes (Table 2.1). In Chlorophytes and Rhodophytes, LICF rarely exceeds 1 μmol $^{14}C\ g^{-1}$ FW h^{-1}, which in terms of their contribution to the photosynthetic carbon is normally $<1\%$ (Cabello-Pasini and Alberte 1997). In the case of brown algae, values can be considerably higher (up to 9.6 μmol ^{14} C g^{-1} FW h^{-1}), accounting for up to 48% of the photosynthetic fixation (Kremer 1981). Especially high LICF rates have been reported in growing thallus areas of Laminariales (e.g., *Laminaria* and *Lessonia*) and during the spring/summer season for temperate and cold-temperate species. In the case of temperate red and brown algae, values of LICF can also be important (Cabello-Pasini and Alberte 1997). Carboxylation measured as the activity of PEP-CK is also linked to growth requirements, especially in species with marked seasonality in growth and photosynthetic carbon fixation, e.g., polar seaweeds (Weykam 1996; Weykam et al.

1997; Wiencke et al. 2009). Interestingly, algae from cold regions have exploited very efficiently the potential for LICF as a strategy to minimize the carbon losses due to high respiration and to optimize the supply of carbon skeletons during rapid growth during the short open water season (Drew and Hastings 1992; Gómez and Wiencke 1998) (see below). For example, in the kelp-like Antarctic brown alga *Ascoseira mirabilis*, LICF represents approximately 9.5% of light C-fixation (Gómez et al. 1995a, b), which is comparable to ratios found in species of *Laminaria* (Küppers and Kremer 1978) (Table 2.1). Despite the potential for LICF that seaweeds exhibit, it is not clear whether this pathway may compensate for C losses due to respiration as pointed by Kremer (1981). Thomas and Wiencke (1991) did not conclusively demonstrate its relationship with dark respiration in several Antarctic marine algae. In general, LICF was between 4.9 and 31% of dark respiration in five brown algae and one red alga. In species such as *Himantothallus grandifolius* and *Desmarestia anceps*, low LICF values were coupled with high respiration rates (Thomas and Wiencke 1991). This situation confirms the findings reported in *Ascophyllum nodosum* where a net C loss due to respiration was estimated in the dark (Johnston and Raven 1986). Recent studies revisiting the role of LICF in carbon metabolism of seaweeds have demonstrated that these reactions can be functional to morpho-physiological strategies to cope with, e.g., enhanced solar UV radiation. In blades of *Lessonia nigrescens*, LICF decreased 70% whereas light carbon fixation decreased by 90% under elevated doses of UV-B radiation. This suggests that LICF could be regarded a compensating mechanism necessary to keep physiological performance of algae during severe photodamage (Gómez et al. 2007). The findings that LICF is also well expressed in temperate and polar Rhodophytes such as *Cryptopleura lobulifera*, *Palmaria decipiens*, and *Iridaea cordata* (Thomas and Wiencke 1991; Weykam 1996; Weykam et al. 1997; Cabello-Pasini and Alberte 1997) open questions related with its involvement in morpho-functional processes that allow these organisms to cope with stressful conditions. Involvement of LICF as a mechanism to reduce photorespiration has only been reported in the Chlorophyte *Udotea* (Reiskind et al. 1988). For most of seaweed groups, especially green and red algae, data on LICF are lacking and thus further studies are required in order to outline accurate conclusions on the significance of this pathway for the ecology of seaweeds.

2.5 Morpho-functional Aspects of Carbon Metabolism

Carbon metabolism in seaweeds is integrated in multicellular organization that in many groups exhibits several plant-like traits. Although seaweeds do not display the structural complexity of vascular plants, the integration of form and function is an important factor even in the simplest groups, e.g., uncorticated filaments and sheet-like species. Thus, gross morphology of seaweeds has been related with ecophysiological adaptations (especially photosynthetic performance and carbon production) in response to abiotic and biotic determinants (Littler and Littler 1980;

Steneck and Watling 1982). It is now well established that thallus morphology defines much of the carbon physiology of large brown and red algae as well as some siphonal Chlorophytes.

2.5.1 The Role of Storage Carbohydrates

Storage carbohydrates of seaweeds are normally formed in the chloroplasts. Starch, a common compound of Chlorophyta and plants, is an insoluble storage polysaccharide constituted by units of ADP-glucose, which is synthesized from the triose phosphate generated in the Calvin–Benson cycle. Alternatively, triose phosphate can be exported via an antiport system to the cytosol to form sucrose. A significant part of the pool of sucrose is recycled to RuBP and thus the formation of starch or sucrose in the cell is a highly regulated process, closely synchronized with the carbon requirements of the Calvin–Benson cycle (Nelson and Cox 2004). The D-glucose monomers are linked to form branched polymers of starch composed of two types of chains: α 1,4-D-glucans (amylose) and/or additional α-1,6-D-glucans (amylopectin). In Rhodophyta, carbohydrates synthesized from carbon fixation are stored as floridean starch, which is characterized by α 1,4-D and α 1,6-glucans. The brown algae have storage laminaran (β-D-glucopyranose), a combination of soluble and insoluble chains of the type β-1,3 and β-1,6-D-glucans. Seaweeds contain also important amounts of low-molecular-weight compounds such as sucrose (green algae), mannitol (which can form part of laminaran chains of brown algae), and floridoside (red algae). These compounds are not only reserve products but also have a series of intracellular functions (e.g., osmolytes; see also Chap. 5 by Karsten) or are also precursors of cell wall polysaccharides (reviewed by Craigie 1974; Wëiwer et al. 2008).

Seasonal variation in major organic compounds, especially carbohydrates, is well known since 60 years and primarily based on studies of large brown algae, especially Laminariales and Fucales (Black 1950; Haug and Jensen 1954; Jensen and Haug 1956) and some Rhodophyta (Dawes et al. 1974). Although these changes were related to gradients of environmental variations (salinity, temperature, light, etc.), the importance of these compounds in life strategy, morpho-functional processes, and stress tolerance mechanisms was addressed later. Only after the classic works by Chapman and Craigie (1977, 1978), the relationship between nutrient availability, growth, photosynthesis, and organic composition in Laminariales could be comprehensively understood. In these seaweeds, degradation of storage carbohydrates, which are built up in summer (when net photosynthetic C assimilation occurs), supplies the energy requirements for growth during high nutrient availability in winter-early spring (Hatcher et al. 1977). In species such as *Saccharina latissima*, mannitol and laminaran vary from total absence in winter (4.5 and 0% DW, respectively) to high values close to 26% DW in summer (Black 1950). This strategy is extreme in the Arctic species *Laminaria solidungula*, which grow only in darkness in winter powered by the carbohydrates (laminaran/mannitol) synthesized during the previous season. About

25% of the original carbon content of the thallus is depleted during the dark winter period while it completes nearly 90% of its annual linear growth (Dunton and Schell 1986). In Antarctic brown algae, due to the seasonally constant levels of nutrients, the dynamics of synthesis and utilization of storage carbohydrates mostly depend on the availability of light. In Antarctic Desmarestiales and Ascoseirales, depletion of laminaran during spring and summer results in increases of mannitol, suggesting that these compounds support requirements during lamina elongation (Drew and Hastings 1992; Gómez and Wiencke 1998; Wiencke et al. 2009).

In cold-temperate and Arctic Laminariales, the significant direct relation between seasonal changes of amino acids to mannitol and the inverse relationship between amino acids and laminaran content confirms that N availability regulates remobilization of stored carbon (Lüning et al. 1973; Küppers and Kremer 1978; Cagné et al. 1982). In the northern hemisphere, high ambient N supply in winter exceeds substantially the N requirements for protein and amino acid synthesis and free N is accumulated in surplus (Chapman and Craigie 1977). In the case of Antarctic algae, seasonal changes in mannitol and laminaran seem to be mainly triggered by daylength, as seasonal carbon budget of *Himantothallus grandifolius*, *Ascoseira mirabilis*,, and *Desmarestia menziesii* is not affected by nutrients in summer like in *Laminaria* (Drew and Hastings 1992; Gómez and Wiencke 1998; Gómez et al. 1995b; Gómez and Wiencke 1998). As for kelps, Antarctic algae suffer a photosynthetic carbon deficit during the growth period, i.e., carbon losses due to anabolism and dark respiration exceed photosynthetic carbon fixation, which may be compensated by reutilization of storage carbohydrates (Gómez and Wiencke 1998). In any case, daylength-dependent variations of storage carbohydrates have been documented in cultured *Laminaria hyperborea*, a species exposed generally to a severe *N* limitation in summer (Schaffelke 1995). Furthermore, exposure to constant short day alters the seasonal growth cycle of *Laminaria digitata* by preventing the decrease of growth rates in summer (Gómez and Lüning 2001), suggesting that not only nutrients but also photoperiodic responses are crucial in carbon metabolism in this group of algae.

Figure 2.1 describes a model of synthesis, remobilization, and utilization of storage carbohydrates during the growth phase for Laminariales. Laminaran, which is built up mainly in distal regions of various species of kelps (Küppers and Kremer 1978; Lüning 1979; Cabello-Pasini and Alberte 2001a), is degraded with release of mannitol, which is transported (along with various amino acids) via translocation to the meristematic region (see below). Mannitol enters in the LICF pathway as a precursor of 3-phosphoglycerate (PGA), which is transformed to phosphoenol pyruvate (PEP) in the mitochondria. One molecule of mannitol generates two molecules of PEP: one can be converted to oxaloacetate (OAA) by the enzyme PEP-CK following the biosynthetic pathway in the Krebs cycle while the other is transformed to acetyl-CoA by the successive action of pyruvate kinase (PK) and pyruvate dehydrogenase (PD) with loss of one molecule of CO_2, which is saved by PEP-CK (Kremer 1981).

The glycolysis of mannitol, as well as the ^{14}C labeling of carboxylic diacids (e.g., malate, aspartate) in the meristematic zones of the blade, has unequivocally confirmed that growth in large brown algae can be supported by nonphotosynthetic,

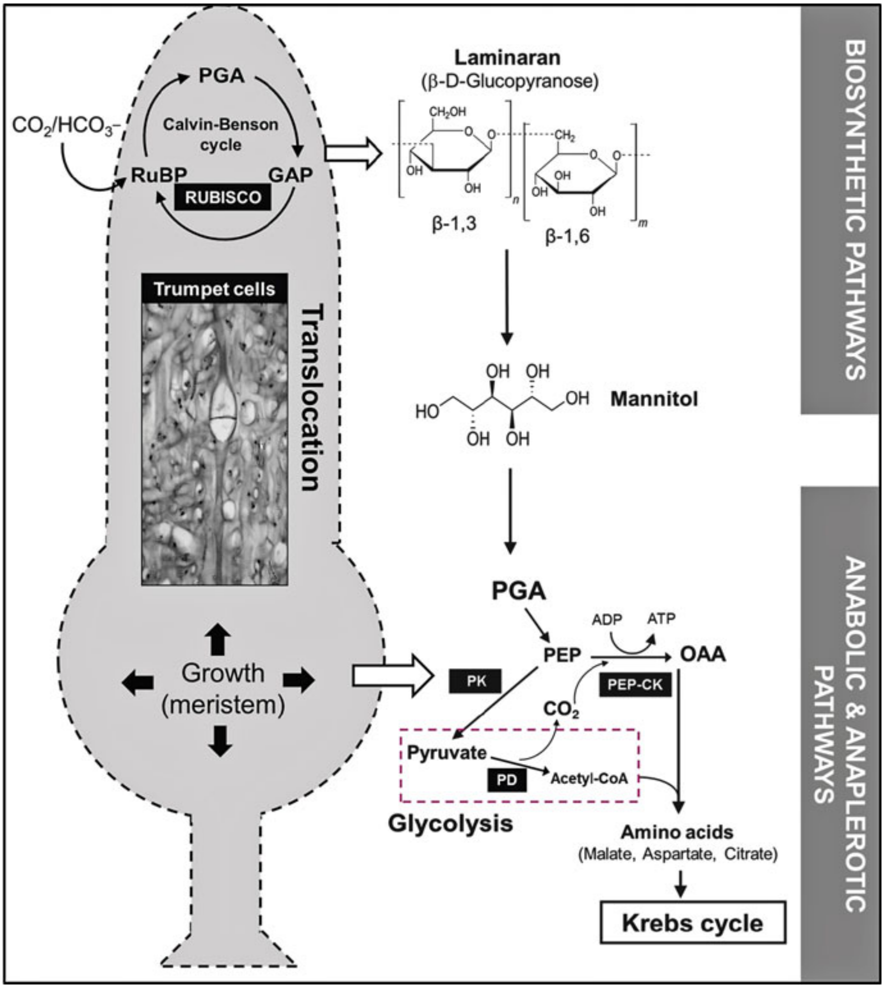

Fig. 2.1 Schema indicating the morpho-functional processes during active growth in Laminariales. In distal thallus regions, photosynthetic carbon fixation via RUBISCO and biosynthetic processes in the Calvin–Benson cycle are connected through translocation of low-weight molecular sugars (e.g., mannitol) with anaplerotic processes mediated by LICF in the intercalary meristem. *PGA*, 3-phosphoglycerate; *GAP*, glyceraldehyde-3-phosphate; *PK*, Pyruvate kinase; *PD*, Pyruvate dehydrogenase; *PEP-CK*, Phosphoenolpyruvate carboxykinase; *PEP*, Phospoenolpyruvate; *RuBP*, ribulose 1,5-bisphosphate

anaplerotic reactions (Kremer 1981; Cabello-Pasini and Alberte 2001b). In Rhodophyta, anaplerotic consumption of storage carbohydrates has been less studied. In *Gelidium coulteri* grown under *N* starvation, rates of LICF were relatively low (1–7%), floridoside was rapidly consumed in glycolysis, and an important fraction of the ^{14}C labeling was allocated to amino acids of the tricarboxylic acids cycle (Macler 1986). This pattern has been found in other Rhodophyta and apparently indicates that, while present, the LICF pathway has much less importance in the whole carbon assimilation in temperate algae (Cabello-Pasini and Alberte 2001b). However, results from the two contrasting polar red algae, the endemic *Palmaria decipiens* and the widely distributed *Iridaea cordata*, indicated that accumulation of floridean starch allows the first species to overwinter in darkness. In the case of *Iridaea*, use of floridean starch to power growth was less marked. In both cases, LICF accounting for up to 9% of the total carbon assimilation was active during a part of the dark period (Weykam et al. 1997), suggesting that nonphotosynthetic carbon metabolism in Rhodophyta may have similar ecophysiological importance in extreme environments as has been reported for large brown algae (Wiencke et al. 2009).

2.5.2 Thallus Anatomy and Long-Distance Transport of Photoassimilates

Unlike vascular plants, where long-distance transport represents the exchange of resources between genuine, highly differentiated tissues, the transport of substances in seaweeds, called translocation, is normally a strategy to redistribute via mass flux diverse organic compounds towards zones of high metabolic activity (Lüning et al. 1973; Schmitz 1981). In Laminariales and Fucales, carbon metabolism is spatially separated in carbon "source" and "sink" regions (Küppers and Kremer 1978; Arnold and Manley 1985; Cabello-Pasini and Alberte 2001a). As is shown in Fig. 2.1 for Laminariales, photoassimilates are stored in the mature, commonly distal regions of the algae, and then transported as mannitol and amino acids to the meristematic region. This morpho-functional arrangement is a consequence of the allometric growth and the action of an intercalary meristem that normally results in tissues with different metabolic activity.

Different types of sieve elements, such as the "trumpet" cells, have been identified in members of Laminariales and Phyllariaceae (Buggeln 1983; Schmitz 1981; Gómez et al. 2007). These structures are formed by specialized, normally vacuolated cells that are longitudinally arranged in the medulla or below the cortex in parenchymatous and peudo-parenquimatous thalli. Cell lengths measured in different Laminariales vary considerably and can reach several millimeters. Most of the sieve tubes end in the so-called sieve plates, which present pores of up to 100 nm diameter permitting the connection between adjacent cells (Schmitz 1990).

Apart from Laminariales, other groups of seaweeds have been shown to have sieve elements or at least a translocation function has been hypothesized. This is the case of the Antarctic genera *Ascoseira* and *Himantothallus*, whose advanced structural organization resembles that of *Laminaria* species from the northern Hemisphere. For example, members of the Ascoseirales are characterized by a strap-like lamina with an intercalary basally located meristem forming new tissue during each growth phase. Thus, the blade in this species is formed by tissues differing in age and developmental stage (Gómez et al. 1995a; Gómez et al. 1996). Histological studies have revealed the presence of medullar structures denominated “conducting channels”. Apparently, putative translocation could occur only in young plants, as early “conducting channels” are metabolically active, possess plasmodesmata, and contain relatively few physodes (Clayton and Ashburner 1990). Long-distance transport of substances has also been documented in members of the brown algal orders Scytosiphonales (Guimaraes et al. 1986), Desmarestiales (Moe and Silva 1981; Wiencke and Clayton 1990), and Fucales (Moss 1983). In Rhodophyta, evidence for translocation of photoassimilates using ^{14}C labeling has been obtained in *Polysiphonia* sp. (Wetherbee 1979), *Delesseria sanguinea* (Hartman and Eschrich 1969), and *Gracilaria cornea* (Gonen et al. 1996). Although the structures and probably the mechanisms of translocation in red algae are different compared to brown algae, a relationship between carbon fixation and translocation has been clearly demonstrated in *Gracilaria* (Gonen et al. 1996).

2.5.3 Patterns of Carbon Allocation

Large and complex seaweeds show a differential allocation of carbon fixation products along the thallus. Various brown algal genera such as *Sargassum* (Gorham and Lewey 1984), *Macrocystis* (Wheeler and North 1981; Gerard 1982), *Lessonia* (Percival et al. 1983; Westermeier and Gómez 1996), *Durvillaea* (Cheshire and Hallam 1985; Lawrence 1986; Gómez and Westermeier 1995), and *Desmarestia* (Carlberg et al. 1978) show longitudinal variation in organic composition. Primarily, changes in carbon allocation can be directly caused by differential capacity for carbon uptake among parts of thallus. Using $^{13}C/^{12}C$ ratios ($\delta\ ^{13}C$), it was possible to identify active HCO_3^- uptake sites along the thallus of Antarctic seaweeds correlated to growth activity (Wiencke and Fischer 1990, 1992). For example, $\delta^{13}C$ values between -12 and -16.8% (indicating ^{13}C enrichment) were measured in new blade regions of *Ascoseira mirabilis* during high irradiances and summer daylength (Gómez 1997). Apparently, enhanced carboxylation rates during high light compensate for the energy costs of active HCO_3^- incorporation by decreasing the C supply via diffusive CO_2 entry, and thus the heavier C isotope is preferentially assimilated (Kübler and Raven 1994; Raven et al. 1995). On the other hand, changes in light use and carbon fixation efficiency along with increasing thallus size and age affect the carbon uptake and allocation. In cultures of *Desmarestia menziesii,* $\delta\ ^{13}C$ values $>-29\%$ were found in small algae, but with increasing size, $\delta\ ^{13}C$ signatures increased accordingly (-32%) (Gómez 1997).

Hydrodynamic processes regulate also the allocation of photoassimilated carbon in the thallus. In many large brown algae, carbon (normally in the form of structural carbohydrates) is preferentially allocated in the basal structures, which are biomechanically designed to attach algae to the substrate and to withstand drag forces from water movement (Hurd 2000). In the fucoid *Durvillaea antarctica,* characterized by large and floating laminar blades, 85% of the total energy contents from organic compounds is allocated to fronds, while the rest is allocated to the holdfast (Lawrence 1986). In the case of the kelp *Postelsia palmaeformis*, 63% of the total organic carbon is allocated to holdfast and stipe, which is in line with a gross morphology designed to resist the direct impact of waves (Lawrence and McClintock 1988). In the southern kelp *Lessonia nigrescens,* carbon allocation changed with increasing size and age: adult plants deposited higher proportion of energy in the holdfast and stipes than young plants with important consequences for population density and local demography (Westermeier and Gómez 1996).

Differential allocation of organic carbon along the thallus can also be functional to withstand other environmental stressors (Wakefield and Murray 2009). The optimal defense theory (ODT) has been proposed to understand the mechanisms that control the interaction between algal allocation of organic compounds and the action of, e.g., herbivores (Cronin and Hay 1996). For example, secondary metabolites are normally allocated in the structures with high fitness value, probably where the investment in energy is higher (Pansch et al. 2008). In brown algae, phlorotannins may function as deterrents for many grazers, but additionally, due to their primary role as cell wall precursors, these compounds act also as cell-wall hardening, conferring mechanical resistance and toughness (Lucas et al. 2000). In the intertidal kelp *Lessonia nigrescens*, holdfast and stipes contain higher concentrations of phlorotannins, and hence are better defended than transient fronds (Gómez et al. 2005; Gómez and Huovinen 2010, see also Chap. 8 by Iken).

Carbon fixation, biomass, and overall the sum of the morpho-functional processes of seaweeds define much of the primary productivity and energy fluxes in the coastal ecosystems (Mann 1973). Due to their size and patterns of substrate occupation, seaweeds represent habitat for other organisms and also modify the physical and chemical environment (Jackson 1998; Delille et al. 2000). In coastal areas of cold-temperate and polar regions, seaweeds can account for >50% of the total fixed carbon (Gattuso et al. 2006). The outcome of seaweed carbon metabolism is transferred to the food web not only via direct consumption by herbivores but also as secondary product via detritus in near shore (Duggins et al. 1989) and abyssal areas (Wiencke and Fisher 1992).

2.5.4 Concluding Remarks

Overall, carbon metabolism of seaweeds is highly versatile and has allowed these organisms to thrive in all types of habitats and environmental conditions. However, despite the considerable advances in our knowledge on mechanisms and pathways, the ecological consequences of many photosynthetic adaptations are not well understood. For example, carbon acquisition patterns in relation with morpho-physiological processes, biomass allocation, reproduction, and development of adult and early stages of seaweeds have been hitherto overlooked (Raven 2003). The significance of endogenous processes regulating carbon metabolism, which has been studied in few brown algae, is also a relevant topic that should be expanded to other seaweed groups in order to gain insights into possible evolutionary issues (Schmid et al. 1996). Probably, one of the most important issues in seaweed physiology will be the understanding of the complex interaction between the expression and modulation of carbon metabolism, and processes underlying large biogeographical patterns of seaweeds. For many aspects related to regulation of carbon metabolism in seaweeds, proteomic and genomic studies are urgently needed and fundamental in order to understand the role of seaweeds in present and future scenarios of global change.

The consequences of increasing CO_2 levels and related phenomena such as the ocean warming and ozone depletion on seaweed ecophysiology have begun to be explored and different surveys describe various biological and geochemical scenarios modified by anthropogenic activities (Israel and Einav 2010). Due to the dependence of RUBISCO on CO_2, it has been postulated that photosynthetic organisms will respond positively to present and future increases in atmospheric CO_2 (Amthor 1995). However, some experimental evidence suggests that large increases in photosynthetic carbon fixation are not expected mainly because most of the studied seaweeds exhibit CCMs (Gao et al. 1993; Beer and Koch 1996; Israel and Hophy 2002). Apparently, the focus could be on the increased competiveness of algae without or with poorly developed CCM, which will depend on a series of other environmental and geographic factors (Raven et al. 2002). Overall, although the studies compiled here give important insights into the potential responses of organisms, the central question whether the mechanisms exploited by seaweeds today allow them to adapt to future scenarios remains open.

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Chapter 3
Seaweed Responses to Temperature

Anja Eggert

3.1 Introduction

“Why don’t seaweeds spread beyond their present boundaries along an uninterrupted rocky coastline?”, asked Breeman in 1988. Two principal aspects play a central role in shaping biogeographical distribution patterns: temperature-dependent effects on performance (e.g., growth, photosynthesis) and temperature tolerance (i.e., survival). The temperature responses of species are often correlated with the local thermal environments, i.e., species are locally adapted, but may vary seasonally or among populations or life stages due to phenotypic plasticity. Accordingly, it is necessary to differentiate three types of temperature responses: (1) genetic adaptation to local conditions, (2) phenotypic acclimation in response to variation of environmental conditions, and (3) short-term physiological regulation. The responses take place over different timescales: seconds to minutes (regulation), hours to days (acclimation), and up to thousands of millions of years (adaptation). This chapter reviews the temperature responses of seaweeds and their biogeographical implications.

3.2 Local Temperature Adaptation of Growth and Photosynthesis

The effect of temperature on performance traits, such as growth and photosynthesis, is typically visualized using temperature–response curves. Both growth and photosynthetic rates of seaweeds increase with temperature, plateau at a maximal level,

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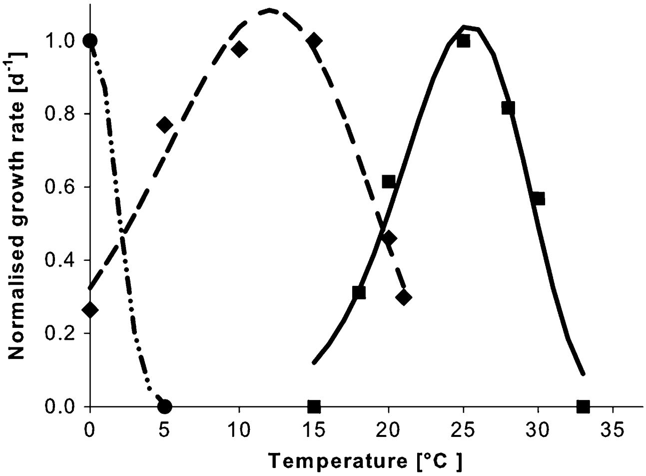

Fig. 3.1 Typical normalized growth temperature–response curves of the stenothermal polar species *Gymnogongrus skottsbergii* (Antarctica, *circles*, Eggert and Wiencke 2000), the eurythermal temperate species *Laminaria digitata* (Helgoland, *diamonds*, tom Dieck 1992), and the tropical species *Wurdemannia miniata* (St. Croix, Caribbean, *squares*, Pakker and Breeman 1996). The temperature–response curves were estimated by fitting the experimental data to the function developed by Blanchard et al. (1996). The temperature optima of the three response curves are 0, 12, and 25°C and the 80%-"performance breadths" are −1–1°C, 7–16°C, and 22–28°C for the Antarctic, temperate, and tropical species, respectively

and then rapidly decline near the upper critical temperature. These temperature–response curves can be characterized quantitatively by estimating various descriptive statistics (e.g., the minimum, maximum, optimum temperature, the performance breadth). Eggert et al. (2003a) introduced the temperature ranges at which 80% and 20% of the maximal growth rate occurs as arbitrary values for "good" and for "sufficient" growth, respectively. This approach intrinsically bypasses the interpretation of the optimum temperature, which is usually a meaningless parameter in the discussion of local temperature adaptation. The "performance breadth" (or alternatively the 80% or 20% temperature ranges) can be interpreted for the concept of eurythermy and stenothermy. Eurythermal seaweeds have a broad "performance breadth" and typically grow in environments with large fluctuations in seawater temperature. In contrast, stenothermal species have a narrow performance breadth and are found in regions with small temperature fluctuations.

Both the "performance breadth" and the position of the growth temperature–response curves of seaweeds typically correlate with the local temperature regime, i.e., reflect local temperature adaptation (Fig. 3.1). The endemic Antarctic species have the longest cold water history of at least 14 Ma (Briggs 1995; Crame 1993; see also Chap. 13 by Wiencke and Amsler) which in turn determines their worldwide lowest temperature requirements (Wiencke et al. 1994; see also Chap. 18 by Bartsch et al.). The red macroalgae *Gigartina skottsbergii* and *Ballia callitricha* grow in a very narrow temperature range between 0 and 5°C (Bischoff-Bäsmann and Wiencke 1996; Eggert and Wiencke 2000). Other Antarctic species with a distribution extending to Tierra del Fuego and subantarctic islands have more eurythermal temperature characteristics. For example, *Gymnogongrus antarcticus* and *Phyllophora ahnfeltioides* grow between 0 and 10°C (Bischoff-Bäsmann and Wiencke 1996; Eggert and Wiencke 2000). Compared to the Antarctic, seaweeds from the Arctic have a shorter cold water history of about 3 Ma (Briggs 1995) which explains the less cold-adapted and more eurythermal characteristics of Arctic species. For example, sporophytes of the kelp *Laminaria solidungula* grow between 0 and 15°C with an optimum at 5–10°C (tom Dieck 1992). Temperate species exhibit the widest performance breadth as they experience largest seasonal temperature changes. Cold-temperate Northeast Pacific and North Atlantic species grow between 0 and 18(20)°C with optima between 5 and 15°C (e.g., Bolton and Lüning 1982; Lüning and Freshwater 1988; tom Dieck 1992; Wiencke et al. 1994), while warm-temperate Atlantic species grow at up to 23–24°C and have slightly elevated optima (e.g., tom Dieck and Oliveira 1993). Additionally, life history stages (i.e., macrothalli/microthalli) of temperate seaweeds with a heteromorphic life history often have different temperature–response curves leading to an overall eurythermal temperature adaptation of the species (tom Dieck 1993). Tropical seaweeds from the Indo-West Pacific have the highest temperature optima of growth at 25–30°C (Pakker and Breeman 1996; Bischoff-Bäsmann et al. 1997).

Similar to growth, photosynthetic temperature responses also reflect adaptation to the local temperature regimes. Seaweeds from colder environments reach higher photosynthetic rates at low temperatures, while seaweeds native to warmer environments exhibit superior photosynthetic rates at higher temperatures. Optimum temperatures for photosynthesis are lowest (10–20°C) in Antarctic macroalgae (Wiencke et al. 1993; Eggert and Wiencke 2000), intermediate (20–25°C) in cold-temperate to Arctic species, and highest (25–35°C) in warm-temperate to tropical species (Terrados and Ros 1992). Thus, temperature optima of photosynthesis are situated well above the temperature optima of growth (Davison 1987; Kübler et al. 1991; Eggert and Wiencke 2000; see also Chap. 13 by Wiencke and Amsler). This shows that temperature effects on a specific physiological process (i.e., photosynthesis in this case) do not necessarily correspond to the temperature–growth pattern as growth integrates the effect of temperature on the total metabolism.

As a consequence of the long cold water history of the Antarctic Ocean, very specific adaptations have evolved in endemic Antarctic species. Eastman (1993) detected "DNA decay" in Antarctic fish, i.e., loss of genetic information not required for life at ambient temperatures (Hoffmann and Willi 2008). Ice-binding proteins have been found in Antarctic sea ice diatoms as a very specific adaptation to the very low, freezing temperatures in this extreme habitat. The extracellular proteins are associated with the diatom community and they serve to prevent freezing injury (Janech et al. 2006). However, it has not been investigated whether these or other types of low-temperature adaptation have evolved in polar seaweeds as well.

Temperature limitations of growth and photosynthesis are a direct effect of temperature sensitivity of the main cellular components, i.e., proteins and membranes. Evolutionary adaptation to local temperatures on the cellular level can involve one or more of the three strategies: quantitative (changing the concentrations of enzymes and/or reactants); qualitative (using a protein variant/ isozyme with different thermal characteristics); or modulation (modifying the protein environment to minimize the impact of temperature change) (Hochachka and Somero 2002). The most important adjustments include changes in enzyme concentration, changes in primary structure affecting the free energy of activation, and modification to both membrane properties and intracellular milieu. These responses are genotypic, but similar changes may be induced by acclimation on a daily or seasonal timescale. The energetic costs of the different strategies of temperature adaptation vary (Clarke 2003). If protein variants/isozymes vary by only a few amino acids, it costs an organism effectively no more ATP to make a molecule of one variant than it does to make another. However, energetic costs become relevant when a particular protein is required in larger amounts, or is turned over faster. Trade-offs with other metabolic processes and changes in energy budgets need to take place. These aspects have been analyzed in polar ectothermic marine animals (Pörtner et al. 2005), but remain to be investigated in polar seaweeds.

Specific knowledge of thermal physiology of proteins is limited to a very small subset of proteins. Clear patterns of adaptive variation have been discovered in structural and functional properties of proteins from ectothermic marine animals adapted to different temperatures (Somero 2004). Studies of dehydrogenase enzymes have demonstrated that a single amino acid substitution is sufficient to cause temperature-adaptive changes in function and stability and define species geographic boundaries (e.g., Fields and Houseman 2004; Dong and Somero 2009). Studies on temperature adaptation are missing for seaweeds and are scarce for unicellular algae. Descolas-Gros and De Billy (1987) showed that the RuBisCO in marine Antarctic diatoms effectively binds CO_2 only at low temperatures. They describe qualitative changes, i.e., an isozyme with modified kinetic properties which allows the maintenance and regulation of RuBisCO activity in Antarctic diatoms at low temperatures (minimum K_m value at 4.5°C for Antarctic species compared to 20°C for temperate species). In contrast, Antarctic *Chloromonas* species did not show an increase in activity at low temperatures (0–5°C) compared to temperate species, which was counterbalanced by increasing enzyme concentration, i.e., quantitative adjustments (Devos et al. 1998).

In addition to proteins, several physical properties of membranes are temperature sensitive, including permeability characteristics, fluidity, and membrane phase state (for reviews, see Murata and Los 1997; Los and Murata 2004). All are crucial to many membrane functions, including the activities of enzymes. A number of studies focused on the effects of low temperature and clearly demonstrated that membrane fluidity decreases with a decrease in temperature (Szalontai et al. 2000; Inaba et al. 2003). The effects of high temperature on the physical state of membranes have also been studied, albeit less intensively (Carratù et al. 1996;

Vigh et al. 1998). High temperatures cause an increase in the fluidity of membranes, which ultimately leads to a disintegration of the lipid bilayer.

The impairment of photosynthesis at low temperature appears to be primarily related to impaired synthesis and functioning of photosynthetic pigment–protein complexes (Robertson et al. 1993; Nie et al. 1995) and reduced activities of key enzymes in the Calvin cycle (Holaday et al. 1992; Huner et al. 1993; Kingston-Smith et al. 1997). There are also several target sites for the impairment of photosynthesis at high temperatures, such as the CO_2 fixation system, photophosphorylation, the electron transport chain, and the oxygen evolving complex (Sharkey 2005; Allakhverdiev et al. 2008). Especially various parameters of fast chlorophyll fluorescence transients of photosystem II, such as the maximum and effective quantum yield (Fv/Fm, Φ PSII), the minimum fluorescence (Fo), and photochemical and non-photochemical quenching of chlorophyll fluorescence, have been widely used to monitor temperature-induced changes of photosynthetic activity in seaweeds (e.g., Antarctic *Palmaria decipiens*, Arctic *Fucus distichus*: Becker et al. 2009, warm-temperate *Valonia utricularis*: Eggert et al. 2003b, tropical to warm-temperate *Laurencia* spp.: Padilla-Gamiño and Carpenter 2007).

3.3 Phenotypic Temperature Acclimation of Growth and Photosynthesis

Most seaweeds have the ability to acclimate growth and photosynthesis in response to changes in ambient temperature, both to daily temperature changes and on a seasonal timescale. Beneficial phenotypic acclimation (*sensu* Leroi et al. 1994) is the improvement of a thermal trait (e.g., growth, photosynthesis) at the respective ambient temperature that allows to maximize performance over a broad temperature range. The potential for temperature acclimation varies between species and is expected to be higher in eurythermal than in stenothermal species. Accordingly, seaweeds native to habitats with large annual temperature variations typically display a stronger ability to acclimate than species from habitats with more stable seasonal regimes. Seasonal acclimation of photosynthesis has been described for seaweeds from the temperate regions (Davison 1987; Kübler and Davison 1995; Pfetzing et al. 2000; Eggert et al. 2006; Padilla-Gamiño and Carpenter 2007). Likewise, acclimation has been described in a number of intertidal species (Smith and Berry 1986; Kim et al. 2009; Henkel et al. 2009). In contrast, a limited acclimation potential has been described for Antarctic and tropical species (Eggert and Wiencke 2000; Eggert et al. 2006).

The fact that temperature changes can induce cellular acclimation responses indicates that temperature is sensed and that the temperature signal is immediately transduced into the cell. Membrane fluidity, protein conformation, cytoskeleton depolymerization, and metabolic reactions have all been identified to be temperature sensors (Horvath et al. 1998; Los and Murata 2004). Enzyme adjustments to temperature occur constantly as temperature changes on different timescales,

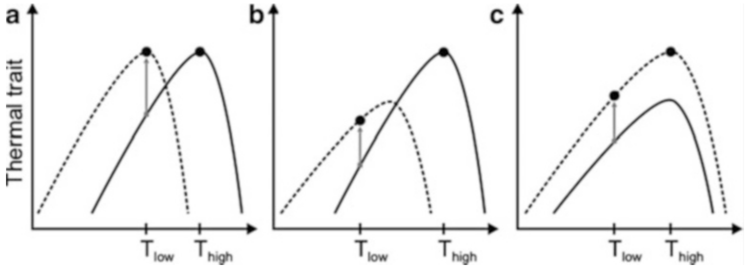

Fig. 3.2 Two individual temperature–response curves of organisms grown at a high temperature T_{high} (*solid line*) and at a low temperature T_{low} (*dashed line*). The *circles* mark the physiological rate at the respective growth temperature. The *gray arrows* indicate (partial) acclimation at T_{low}. (**a**) "Complete low-temperature acclimation", (**b**) "Beneficial acclimation hypothesis", and (**c**) "Colder is better hypothesis"

e.g., diurnally or seasonally. The quantitative and/or qualitative metabolic adjustments of proteins that allow temperature compensation are similar to the genotypic evolutionary adjustments (Clarke 2003). Also, membranes can undergo changes in both lipid composition and degree of unsaturation of fatty acids in response to temperature changes. In this way, they can maintain a relatively constant fluidity and can alter the state transition temperature (Los and Murata 2004). These homeoviscous changes are very important in establishing the appropriate membrane physical state for some enzymes at different temperatures.

Phenotypic acclimation can be tested experimentally by comparing temperature–response curves (short-term effects) of organisms grown at different temperatures (long-term effects). The following three parameters of the short-term temperature–response curves are the most important: maximum rate, temperature optimum, and performance breadth. Both a shift in the response curve (including temperature optimum) and increase in maximum rate may be beneficial and maximize performance over a broad temperature range. Various acclimation hypotheses are discussed in evolutionary biology (Deere and Chown 2006). "Complete temperature compensation" maintains the physiological rates as the temperature changes (Fig. 3.2). However, partial compensation is apparently more common and is predicted from the "Beneficial acclimation hypothesis" caused by some co-variation between optimum temperature and maximum rate and some overlap of the performance curves (Fig. 3.2b). Temperate populations of *Valonia utricularis* (Chlorophyta, Eggert et al. 2006) and *Asparagopsis taxiformis* (Rhodophyta, Padilla-Gamiño and Carpenter 2007) displayed seasonal (partial) temperature acclimation of photosynthesis, whereas tropical individuals of both species did not. Alternatively, the hypothesis "Colder is better" predicts that an organism acclimated to a low-temperature environment will always have a performance advantage over another organism held at a warmer environment (Fig. 3.2c). In this case, the optimal temperature does not change, but the performance curve overall increases. This type of acclimation of photosynthesis has been shown for the Antarctic seaweeds *Ballia callitricha* and *Gymnogongrus antarcticus* (Eggert and

Wiencke 2000) and was also found for cold-temperate specimens of the kelp *Saccharina latissima* (Davison et al. 1991) and the red macroalga *Chondrus crispus* (Kübler and Davison 1995).

Photosynthetic adjustments in response to a change in growth temperature take place in order to counteract the imbalance between photosynthetic energy production and cellular energy consumption (Wilson et al. 2003a). Low-temperature acclimated *Chlorella vulgaris* cells exhibit high chlorophyll *a*:*b* ratio, low light-harvesting complex polypeptide abundance, and an increased zeaxanthin content (Wilson and Huner 2000). Machalek et al. (1996) describe in *Saccharina latissima* a decrease in concentration of major light-harvesting pigments when grown at suboptimal temperatures, and thermal acclimation in *Chondrus crispus* is characterized by variations in antenna size rather than by reaction center densities (Kübler and Davison 1995). Notably, not necessarily all components of the photosynthetic apparatus are sensitive to a temperature change. Wilson et al. (2003a) describe that shifting *C. vulgaris* cells from 5 to 27°C did not induce changes in the accumulation of RuBisCO, a key enzyme of photosynthesis utilizing ATP and NADPH to reduce CO_2 in the Calvin cycle. However, this result contradicts observations by Savitch et al. (1996) and the amount of RuBisCO was also significantly higher in the kelp *Saccharina latissima* when grown at 5°C compared to 17°C-grown algae (Machalek et al. 1996). Acclimation of photosynthesis to high temperatures primarily involves changes in lipid composition of thylakoid membranes and the adjustment of photosystem II thermostability, which could be enhanced either directly through conformational changes of the photosystem or indirectly via a carotenoid-dependent modulation of membrane fluidity (Havaux and Tardy 1996).

It appears that there is more than one cellular signaling mechanism involved in temperature acclimation. There is consensus that the redox state of the plastoquinone pool acts as a sensor of imbalances in the electron transport and is involved in regulating the gene expression of a large number of genes required for photosynthesis (Pfannschmidt et al. 1999). In addition, the *trans*-thylakoid pH gradient, biosynthetic precursors of chlorophyll acting as potential signaling molecules, and reactive oxygen species (see also Chap. 6 by Bischof and Rautenberger) acting as second messenger type molecules have also been shown to be involved (Wilson and Huner 2000; Wilson et al. 2003b). The response of thermal acclimation of photosynthesis appears to be highly comparable to that described for photoacclimation (Huner et al. 1998). However, temperature and light have been shown to have interactive effects on photosynthesis and its regulation (Savitch et al. 1996; Gray et al. 1997).

Today molecular tools such as cDNA and oligonucleotide DNA microarrays ("gene chips") are used for examining environmentally induced changes in the transcriptome. Insights into the role of phenotypic plasticity in transcriptional processes are beginning to be achieved in a variety of species, including Antarctic fishes and invertebrates (Hofmann et al. 2000; Clark and Peck 2009). One major obstacle to studies in seaweeds has been the lack of genomic information, which is now increasing. The genome of the brown macroalga *Ectocarpus siliculosus* has been sequenced by the French sequencing center Genoscope (see http://www.cns.fr) and the Joint Genome Institute (http://www.jgi.doe.gov/) is presently sequencing the complete nuclear genome of *Porphyra umbilicalis*, which is a large eukaryotic genome (haploid genome 5–270 mb; reviewed in Gantt et al. 2010). However, notably large expressed sequence tag (EST) projects on the red alga *Porphyra yezoensis* (Nikaido et al. 2000; Asamizu et al. 2003), but also smaller EST projects on, e.g., the red alga *Chondrus crispus* (Collén et al. 2006), the brown alga *Laminaria digitata* (Roeder et al. 2005) and the green alga *Ulva linza* (Stanley et al. 2005), allow the utilization of powerful tools of functional genomics.

3.4 Disruptive Temperature Stress and Thermal Tolerance

Heat stress and cold stress (including freezing) cause damage to seaweeds and are referred to "disruptive stress" *sensu* Davison and Pearson (1996) due to adverse conditions beyond phenotypic temperature acclimation to suboptimal temperatures. The timescale of disruptive temperature stress is particularly relevant. Organisms may cope temporarily (timescale of hours) with strong temperature stress and subsequently recover from damage at optimal conditions (Eggert et al. 2003b). But on a longer timescale (timescale of weeks) and/or increasingly stressful conditions, the organisms experience progressively more impaired cellular processes until the minimum and maximum temperatures for survival are reached. The degree of physiological dysfunction becomes very severe at these cardinal temperatures and cell death ultimately follows. The individual temperature tolerance of seaweed species defines the minimum and maximum temperatures for survival. Upper and lower temperature limits for survival with biogeographical implications are typically assessed using incubation periods of 2–8 weeks and a recovery phase of 2 weeks at optimal temperatures (e.g., Wiencke et al. 1994; Eggert et al. 2003a).

Short-term thermal stress is severest for benthic algae in the high intertidal, where factors causing desiccation and/or critical temperatures determine the upper limit for growth (Davison and Pearson 1996). Seaweeds that grow in shallow tide pools or are even exposed to air during tidal emersion may regularly experience abrupt temperature changes of 10–20°C (Helmuth and Hofmann 2001). Also, freezing is an important stress for polar and cold-temperate intertidal algal communities (Pearson et al. 2000). Tolerance ranges (i.e., the range between upper and lower lethal temperatures) have been found to be broader in intertidal seaweeds occupying the upper shore than in species from the subtidal (Einav et al. 1995; Stengel and Dring 1997; Martone et al. 2010). Short-term thermal stress on the organism level seems ecologically less relevant for seaweeds growing in the subtidal where algae are virtually always submerged.

Seaweeds growing in the center of their geographic distribution show seasonal variation in biomass that is typically not directly controlled by seasonal temperature stress, but most importantly by the variability of the light regime and the availability of nutrients (Kain 1989; Wiencke et al. 2009). However, thermal stress may limit seaweed growth in all populations growing near distribution boundaries that are set by lethal temperature limits. Notably these boundary populations are threatened by global warming, an issue that is addressed in Chap. 18 by Bartsch et al. Heat stress may limit seaweed growth in tropical regions in summer when high temperatures exceed the upper thermal tolerance limit of seaweeds, which is <35°C in many strictly tropical seaweeds. Pakker et al. (1995) describe experimentally determined upper tolerance limits of tropical Caribbean seaweeds at 30°C or 33°C, i.e., very close to the local summer temperatures of 30°C. Populations of the fucoid seaweed *Sargassum lapazeanum* from the Gulf of California also showed maximal mortality rates coinciding with highest values of seawater temperatures in summer (29–30°C, Rivera and Scrosati 2006). On shallow reef flats in the southern Red Sea, temperatures may even exceed 34°C for prolonged periods in summer and seaweeds strongly decrease in biomass or disappear during the hot season (Ateweberhan et al. 2005). The tropical green macroalga *Cladophora submarina* is restricted in the western Atlantic to the Caribbean and Bermuda. Its northward extension is prevented by lethal, low winter temperatures <15°C (Cambridge et al. 1987). This species may experience severe cold stress very close to the lethal limits for 1–2 weeks during cold winters at the Florida Keys, when temperatures in the shallow bays may fall below 15°C caused by intrusion of polar air masses.

On the cellular level, heat stress is known to affect membrane-associated processes as high temperatures cause fluidization of membranes and finally disintegration of the lipid bilayer (Los and Murata 2004). Also, protein stability and function are impaired and cause decreased enzyme activities or even enzyme inactivation. Moreover, membrane and protein damage trigger the production of reactive oxygen species, which in turn inhibit the de novo proteins synthesis (Larkindale et al. 2005). Specifically with respect to photosynthesis, there are three major heat-sensitive sites: photosystem II with the oxygen evolving complex, ATP generating ATP synthase, and enzymes of the Calvin–Benson cycle (Allakhverdiev et al. 2008). The primary event of cold stress is the formation of lipid gel phases in cell membranes. When a model membrane enters a phase-separated state in which gel and liquid-crystalline phases coexist, the membrane becomes permeable to small electrolytes. This permeability results in the disruption of ion gradients, across the membrane, that are essential for the maintenance of cellular activities (Nishida and Murata 1996). Changes in the ultrastructure of chloroplasts were detected in the green macroalga *Valonia utricularis* when exposed to cold stress (Eggert 2002). Chloroplasts were less dense packed in the warm-temperate Mediterranean isolate and became particularly disorganized and more swollen in the tropical Indian Ocean isolate when algae were grown at 15 and 18°C, respectively (Fig. 3.3). Disorganization of chloroplasts reduces light-harvesting capacity and ultimately photosynthetic activity (Ciamporova and Trginova 1996). As temperature decreases to freezing temperatures, ice forms in the intercellular spaces (Tomashow 1998). The accumulation of ice would result in the physical disruption of the cells. However, freezing injury results primarily from cellular dehydration rather than from direct mechanical damage by ice crystals. Freeze-induced dehydration causes denaturation of proteins, precipitation of various molecules, and multiple forms of membrane lesions (Steponkus and Webb 1992).

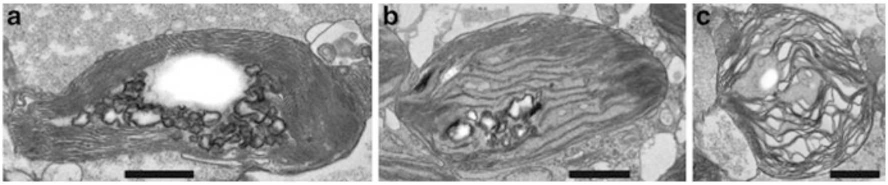

Fig. 3.3 Electron micrographs of cross-sections of *Valonia utricularis* cells, showing chloroplast ultrastructure of the cells. Scale bars measure 1 µm. (**a**) Warm-temperate, Mediterranean isolate grown at optimal temperature (25°C), (**b**) warm-temperate, Mediterranean isolate grown at slight cold stress (15°C), (**c**) tropical, Indian Ocean isolate grown at severe cold stress (18°C). Cells were fixed in situ with 6.0% (w/v) glutaraldehyde in 0.1 M Na-cacodylate buffer (pH 7.2) overnight at 0°C, washed three times with 0.1 M Na-cacodylate buffer (pH 7.2), and postfixed (15 min at room temperature) with 1.5% (w/v) $KMnO_4$. Cells were washed with distilled water and stained in 1.0% (w/v) uranyl acetate overnight. Cells were then dehydrated in an upgrade series of ethanol and embedded in Epon 812 (for more details, see Eggert 2002)

All these types of damage cause reduced photosynthesis and carbon assimilation and ultimately cell dysfunction and cell death.

However, many seaweeds, particularly from temperate regions, can evolve greater resistance to temperature stress via increased tolerance or activation of recovery mechanisms. Both types can serve to extend their temperature range for survival during acute temperature stress. For instance, Davison (1987) reports an acquired high-temperature tolerance of photosynthesis in sporophytes of *Saccharina latissima* grown at 10–20°C compared to specimens grown at 0–5°C due to changes in the thermal stability of the photosystem II electron transport system. Similarly, *Chondrus crispus* grown at summer seawater temperatures (20°C) maintains constant rates of light-saturated photosynthesis at 30°C for 9 h, while photosynthesis of 5°C-grown algae declined rapidly within 10 min following exposure to 30°C (Kübler and Davison 1993). Cold-acclimated (15°C) *Valonia utricularis* exhibited a faster recovery kinetics from chilling-induced photoinhibition than specimens grown at 25°C (Eggert et al. 2003b), which was related to a faster recovery from chronic photoinhibition.

Increased thermal tolerance involves a large suite of processes that modify the cellular metabolism. Again, cellular and molecular investigations in seaweed species are scarce, but the following examples cover a wide range of processes: (1) Heat shock proteins are accumulated as they function as molecular chaperones that protect cellular proteins from protein mis-folding and degradation by environmental stress, including cold and heat stress (Sorensen et al. 2003). Henkel et al. (2009) suggest a high thermal tolerance of the invasive kelp species *Undaria pinnatifida* in the northeast Pacific (California) due to a high expression of the hsp70 gene which encodes heat shock protein 70. (2) The unsaturation of fatty acids increases membrane fluidity and such an increase is necessary if cells are to tolerate cold stress and to survive low temperatures (Murata and Los 1997). Increasing proportions of polyunsaturated fatty acids and, consequently, a higher degree of unsaturation in *Caulerpa racemosa* from the northern Adriatic coincided with a sharp decrease in water temperature in winter (Blažina et al. 2009). By this increased low-temperature tolerance, this species can successfully survive the winter without visible necrotic parts or chilling injuries. (3) As thermal stress disrupts the cellular homeostasis of cells and enhances the production of reactive oxygen species, antioxidants are crucial for increased stress tolerance (Mittler 2002; see also Chap. 6 by Bischof and Rautenberger). Collén et al. (2007) investigated the effects of heat stress on the transcriptome of *Chondrus crispus* using cDNA microarrays. They showed that high-temperature stress caused large changes in gene expression and resource allocation, including antioxidant proteins and detoxifying enzymes. (4) Compatible solutes are accumulated, which are low-molecular-mass, highly soluble organic compounds and are particularly known to serve as osmolytes in salt-stressed cells, including seaweeds (Yancey 2005). The metabolites in seaweeds can include betaines, polyols, and sugars, such as mannitol and trehalose, and amino acids, such as proline (Kirst 1990; see also Chap. 5 by Karsten). Compatible solutes are known to exert multiple protective functions in the metabolism and can also act as antioxidants and can stabilize proteins upon heat stress. Even though similar physiological functions are reasonable to assume in seaweeds as well, they are still to be experimentally proven (Eggert and Karsten 2010).

3.5 Temperature Control of Biogeographical Distribution Boundaries

Geographical distributions of seaweeds are typically delimited at certain seawater isotherms. Based on the historical concept of Setchell (1920) and modified by Lüning (1990), local winter and summer isotherms (i.e., long-term mean monthly temperatures of February and August, respectively) of sea surface temperatures are used for delimitation of biogeographical regions. Seven biogeographical regions are typically recognized in marine phycogeography (for details, see Chap. 18 by Bartsch et al.).

According to van den Hoek (1982a, b) and Breeman (1988), three fundamentally different types of geographic seaweed boundaries can be distinguished: (1) lethal boundaries, i.e., high or low temperatures prevent survival of the hardiest life history stage, (2) reproduction boundaries, i.e., high or low temperatures prevent completion of the life history, (3) growth boundaries, i.e., temperature requirements for sufficient increase of population size. Lethal boundaries are determined by the capacity of the species to survive during the unfavorable season. More specifically, southern lethal temperature boundaries of cold-adapted species (of the Northern hemisphere) are set at the August isotherm of the seawater and the northern lethal limit of warm-adapted species (of the Northern Hemisphere) at the February isotherm. Temperature limits for growth or reproduction operate during the favorable season. Accordingly, southern growth/reproduction limits in the Northern Hemisphere are set at the February isotherm and northern boundaries are determined by the August isotherm. Moreover, seaweed distribution is affected by temperature–daylength interactions (Dring 1984; Molenaar 1996). Optimum temperatures for growth and reproduction or lethal temperatures for the non-hardiest life stage are typically irrelevant in explaining geographic distribution. Suboptimal or sublethal temperatures often prevail at species distribution boundaries. For instance, in case of the tropical to warm-temperate species *Cladophora albida*, which has optimum growth temperatures as high as 25–30°C, temperatures are even suboptimal for year-long growth over a large part of the distribution range at the NW Atlantic coast (Cambridge et al. 1984). Also, many seaweeds from the Arctic grow suboptimally during most of the year and they have a wider distribution in cold-temperate regions (Gómez et al. 2009).

Temperature ranges for survival, growth, and reproduction have been determined experimentally for a large number of seaweed species during the last three decades. Supporting the concepts described above, large-scale biogeographic distribution patterns of many seaweed species were explained by combining the species' thermal traits with local seawater temperatures. Species with similar thermal responses and the same types of distribution boundaries have been assigned to phytogeographic distribution groups (c.f. van den Hoek 1982a, 1982b; Breeman 1988; Wiencke et al. 1994 for designation of groups).

Ecotypic differentiation in thermal responses would be expected in broadly distributed seaweed species, living in a strong thermal gradient. Genetically distinct temperature ecotypes are locally adapted to the particular temperature regime (ecotype definition *sensu* Turesson 1922) and may influence the location of geographic boundaries in a number of species. On the other hand, populations may not be distinct from each other and temperature requirements change gradually over the distribution area, i.e., variation is of an ecoclinal nature. The recognition of ecotypes is intrinsically linked to the definition of species (e.g., Hey 2006), a subject that requires molecular approaches as many seaweed morphospecies are composed of biologically and genetically distinct lineages (Andreakis et al. 2007; Wattier and Maggs 2001; Boedeker et al. 2008). Studies on local adaptation and adaptive evolution in new environments of seaweeds that include molecular data still remain few (Johansson et al. 2003; Bergström et al. 2005; Pereyra et al. 2009; Verbruggen et al. 2009). Most studies on ecotypic differentiation in seaweeds were done with biogeographical isolates, grown under the same laboratory conditions in "common-environment experiments." The temperature responses of thermal traits (i.e., upper and lower survival temperatures, growth range, temperature requirements for reproduction, and photosynthesis) are typically determined and compared with the annual temperature regime of the respective habitats. Especially, the annual growth yield (potential monthly growth rate) is a useful parameter to evaluate local temperature adaptation as it allows to combine the seasonal temperature range with the temperature dependence of growth (e.g., applied in Breeman and Pakker 1994; Bischoff and Wiencke 1995; Eggert et al. 2003a). It is concluded from these "common-environment studies" that observed differences between isolates have a genetic basis and the results provide evidence for intra-specific differentiation. Thermal ecotypes or ecoclinal variation has been described for seaweed species with a disjunct distribution or with wide distributional ranges (Bolton 1983; Bischoff and Wiencke 1995; Pakker and Breeman 1996; Eggert et al. 2003a). In contrast, Pakker et al. (1996) did not find ecotypic differentiation in tropical to subtropical seaweed species with disjunct eastern and western Atlantic populations, despite the large geographic distance. It was suggested that trans-Atlantic dispersal events may be responsible for the lack of ecotype formation. Molecular studies have confirmed the occurrence of long-distance dispersal across the central Atlantic Ocean for a number of seaweed species (Kooistra et al. 1992; Pakker et al. 1996; Pakker and Breeman 1996).

The potential for recent/ongoing geographic differentiation is especially rich on the north-western Atlantic coast, where spatial variability in the environment is strong, with a steep latitudinal gradient in temperature. Differentiation along the north-western Atlantic coast has been found in several marine macrophytes (e.g., *Saccharina latissima*: Gerard and Du Bois 1988). However, the semi-enclosed marginal Mediterranean in the eastern Atlantic also facilitates thermal isolation and selection pressure, processes which appeared especially important during Pleistocene ice ages. Similar marginal seas do not exist in the recent north-western Pacific, even though the Japan Sea might temporarily have also functioned as a warm water pocket during glaciations (van den Hoek and Chihara 2000). *Valonia utricularis*, *Cladophora albida*, and *C. vagabunda* present three examples in which Pacific northern boundaries are situated much further south than Atlantic northern boundaries and which showed ecotypic differences (Breeman et al. 2002; Eggert et al. 2003a).

Biogeographical patterns have long been studied in a rather descriptive way, disregarding that thermal traits are susceptible to evolutionary forces. The rising of molecular data and phylogenetic reconstruction in phycology during the last two decades has led to a number of new research questions related to evolutionary dynamics in biogeography on a species-by-species basis (Avise 2000). Molecular studies put forward evolutionary scenarios to explain the recent distribution of species by considering historical events such as glacial refugia (e.g., *Palmaria palmata*: Provan et al. (2005), *Fucus spiralis*/*F. vesiculosus* species complex: Coyer et al. 2011), vicariance, e.g., due to the rise of the Panamanian Isthmus (*Halimeda* species: Kooistra et al. 2002), or recover historical patterns of seaweed dispersal (*Bostrychia radicans*/*B. moritziana*: Zuccarello et al. 2006). However, many historical biogeographic studies consist of subjective interpretations of genetic and physiological differentiation among geographic isolates. A model-based inference approach is relatively recent and so far not applied for algae (Ree and Sanmartín 2009). Furthermore, sophisticated ecological niche models have been applied in recent years to predict geographical areas with suitable habitat for the species (e.g., Guisan and Thuiller 2005; Raxworthy et al. 2007). So far, species distribution modeling has focussed on terrestrial organisms. Notable exceptions are the study by Graham et al. (2007) which used a niche model to predict kelp habitats in deep tropical waters and the work by Verbruggen et al. (2009) on evolutionary niche dynamics in the green seaweed *Halimeda*. Finally, Tyberghein et al. (2011) presented the data package Bio-ORACLE (Ocean Rasters for Analysis of CLimate and Environment) that permits the development of accurate distribution modeling of marine seaweeds.

3.6 Conclusion

Local temperature adaptation and phenotypic acclimation of performance traits (i.e., growth and photosynthesis) and temperature tolerance ranges (i.e., survival) have been experimentally determined for a wide variety of seaweed species from virtually all biogeographical regions during the last three decades. Large-scale biogeographic distribution patterns of many seaweed species could be explained by combining these thermal traits with local seawater temperatures. In contrast to the vast knowledge on temperature responses of seaweeds on the organism level, studies on temperature effects on cellular components (i.e., proteins and membranes) and environmentally induced changes in transcriptional processes still remain scarce. One major obstacle has been the lack of genomic information of seaweed species, which is now increasing. Furthermore, sophisticated ecological niche models have been applied in the recent years to predict geographical areas with suitable environmental conditions for marine seaweed species.

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Chapter 4
Environment and Algal Nutrition

Francisco J.L. Gordillo

4.1 Introduction

The mechanisms by which macroalgae take up nutrients from the external medium and use them to form biomolecules have been long and widely studied (e.g., Raven 1984; Lobban and Harrison 1994). In this chapter, the focus is on the ecophysiology of these mechanisms for the main nutrients C, N, and P. Particular details on uptake and utilization mechanisms are included when considered ecophysiologically relevant. Physical aspects such as water movement and seasonality are included, nutrient availability is discussed in terms of environmental conditioning of N and P supply for storage and growth, and different species-specific metabolic strategies are presented. Some attention has been paid to the interference of N assimilation with C assimilation pathways. Carbon assimilation is treated more in-depth in Chap. 2 by Gómez and Huovinen. For the interactive effects of ocean acidification on seaweeds, see Chap. 19 by Roleda and Hurd.

Nutrient uptake and assimilation mechanisms are the link between the resources externally available and the demands for growth. However, the environment where macroalgae develop is characterized by strong fluctuations in a number of relevant factors including nutrients, so that macroalgae show some plasticity in terms of resource management and internal composition of the biomass, thus rapidly acclimating to the nutritional conditions. Algae can switch their photosynthetic energy investment from C to N and P acquisition during the course of the day, or from summer to winter. Most remarkably, different mechanisms of resource utilization for different species coexist at the same time in the same community, and this strategy of partitioning brings a more effective resource use, i.e., better transfer to the whole food web.

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The different processes involved in nutrient acquisition follow the terms as used by Berges (1997). Accordingly, uptake is defined as removal of a given molecule or ion from the environment and its physical transport into the algal cell. In macroalgae and higher plants, a further distinction between transport into intercellular spaces and transport into cells themselves may be useful (Redinbaugh and Campbell 1991), but this difference is not considered here. The term assimilation is reserved for the processes by which internalized inorganic molecules are used to form small organic molecules, such as amino acids, and incorporation is defined as the process by which nutrient-containing organic molecules are combined to form macromolecules, such as proteins and nucleic acids, thus participating in growth. These definitions are functional and pragmatic; for example, disappearance of nitrate from the medium can be easily measured, and a separation of small organic and inorganic molecules is relatively straightforward. Note, however, that the enzymatic components of each process are not specified.

4.2 Meeting Nutritional Needs

Nutrient uptake mechanisms must be optimally evolved in order to meet the nutritional needs of a given species in its environment. Algae use light energy to fix carbon (C) and combine the carbon with elements such as nitrogen (N) and phosphorus (P) at relatively constant stoichiometric ratios. C/N/P ratios of unicellular algae are typically around 106:16:1, the so-called Redfield ratio (Redfield et al. 1963), while the C/N/P ratios of benthic plants are larger and more variable, with a median C/N/P ratio of 550:30:1, called the Atkinson ratio (Atkinson and Smith 1983). Falkowski (2000) proposed that the origin of the constant Redfield ratio is a result of a limitation intrinsic to protein synthesis. Atkinson and Smith (1983) proposed that the higher C/N ratio of benthic plants is related to a requirement of structural strength. Baird and Middleton (2004) and Raven and Kübler (2002) discussed the physical limits of nutrient uptake and metabolic rate, respectively, in relation to light absorption. In addition, variability can be further explained by different metabolic strategies and storage capacities (Fujita 1985; Pedersen and Borum 1996).

Regarding uptake kinetics, the extracellular concentrations of many of the chemical species that are required by intracellular assimilation processes are often much lower than the half-saturation value of the transport and/or assimilating enzyme for that chemical species, potentially greatly limiting the rate at which nutrients could be assimilated and used in growth (e.g., Raven et al. 2008). While this situation could, in the general case, be remedied by increasing the quantity of the assimilatory enzyme, the mismatch between the external concentration and the half-saturation value of the assimilatory enzyme can be extreme.

4.2.1 Extracting Nutrients from their Environment

Macroalgae inhabit mostly aquatic environments, and although intertidal species are also exposed to emersion and direct contact with air, nutrients for macroalgal growth are mostly taken from the surrounding water bodies. Benthic communities may be limited by the transport of nutrients through a diffusive boundary layer (Baird and Atkinson 1997; see also Chap. 19 by Roleda and Hurd), by uptake kinetics on the plant surface, or by a combination of the two (Bilger and Atkinson 1995). When limited by transport through a diffusive boundary layer, nutrient uptake rate remains a function of surface roughness and water velocity (Baird and Middleton 2004).

The relatively high viscosity and density of seawater result in drag and acceleration forces on macroalgae that are considerably greater than those experienced by terrestrial plants and restrict the upper size limit to which macroalgae can grow (Gaylord et al. 1994). Rates of molecular diffusion of essential nutrients such as carbon dioxide (CO_2) are 10,000 times slower in seawater than in air (Denny 1990, 1993). Despite this, high production rates of macroalgae indicate the evolution of mechanisms able to overcome this apparently restrictive fluid environment. The main hydrodynamic habitats of macroalgae have been discussed in detail by Hurd (2000).

Intertidal macroalgae are exposed to air and water. On wave-exposed coasts, intertidal and shallow subtidal macroalgae will experience the full force of breaking waves. This multidirectional flow results in the rapid back and forth movement of the thalli, imparting large drag and/or acceleration forces. Intertidal macroalgae also grow in wave-sheltered sites such as bays or estuaries that are protected from ocean waves, and water motion arises predominantly from smaller wind-generated surface waves and the rise and fall of the tide. Some intertidal macroalgae are submerged in rock pools that are isolated from the ocean at low tide. Subtidal macroalgal communities can also be classified as wave-sheltered and -exposed, but subtidal macroalgae do not experience the full force of breaking waves, and the velocities they encounter will often be lower than those of intertidal sites. Relatively calm conditions can occur at both intertidal and subtidal sites that are wave-exposed.

Macroalgae can store nitrogen and phosphorus on a short- (days, e.g., *Chaetomorpha* sp.; McGlathery et al. 1996) or long- (weeks–months, e.g., *Macrocystis*; Brown et al. 1997) term basis. The productivity of a macroalga with a large nitrate storage is, therefore, unlikely, to be limited by short-term reductions (seconds–hours; see discussion below on timescales of velocity fluctuations) in nitrate mass transfer due to slow mainstream velocities. Similarly, photosynthesis can be maintained in the absence of DIC for up to 6 h in *Ulva* (Koch 1993) and 24 h in *Ascophyllum nodosum* (Ryberg et al. 1990) through the utilization of stored DIC. Therefore, under slow mainstream velocities, the degree to which macroalgal production will be reduced will depend on their physiological status, the timescale over which the diffusion boundary layer forms relative to its nutrient requirement, and the ability of the algae to adapt physiologically to the reduced nutrient flux (Hurd 2000).

However, many macroalgae have nutrient sources other than the mainstream seawater which may alleviate nutrient limitation even in slow flows. Benthic algal mats that form in areas of reduced mainstream velocities take up nutrients from the sediment. In fact, macroalgae and benthic microalgae are key factors controlling the fluxes of inorganic and organic N fluxes between the sediment and the water column (Tyler et al. 2003). The high concentration gradient between the sediment and the algal mat may lead to a high nutrient flux (Larned and Atkinson 1997 and references therein). Kamer et al. (2004) found that the relative importance of the water column vs. the sediment as a source of nutrients for *Ulva intestinalis* varied with the magnitude of the different source. Additionally, ammonium and urea are excreted by invertebrates living within the boundary layer on the macroalgal surface (Probyn and Chapman 1983; Taylor and Rees 1998). Gerard and Mann (1979) attributed the high growth rates of a wave-sheltered *Laminaria hyperborea* population to the provision of ammonium from epiphytic bryozoans, an idea supported by the high levels of nitrogen found directly beneath bryozoan colonies on *Macrocystis integrifolia* (Hurd et al. 1994). Similarly, macroalgae may obtain carbon dioxide released from respiration by bryozoans (Muñoz et al. 1991; Mercado et al. 1998).

Another physical determinant on macroalgal nutrition is the algal surface area to biovolume ratio (SA:V), especially at low concentrations (Rees 2007). Hein et al. (1995) suggested that N and P uptake rate and maximum capacity ($V_{\max}$) in algae is, at least in part, linked to their SA:V, so that algae with low SA:V show lower uptake efficiency and $V_{\max}$ values than algae with high SA:V at both low and high nutrient concentrations. Rees (2003), however, found no relationship between the affinity constant (K_m) and SA:V for nitrate, ammonium, and phosphate uptake in macroalgae. Light reaching macroalgae is (mainly) a two-dimensional phenomenon while nutrient uptake and use is three-dimensional. Baird and Middleton (2004) studied the relationship between light and N requirements and suggested that for benthic plants the rates of light absorption to nutrient uptake varies depending on both plant morphology and hydrodynamic conditions.

4.2.2 Neutral vs. Ionic Nutrients

Most nutrients are in ionic form, impermeable to the lipidic plasma-membrane. Main exceptions are inorganic carbon in the form of CO_2 and ammonia, NH_3, which can penetrate the cell with fluxes of 7–18 mm s^{-1} and 6–7 mm s^{-1}, respectively (Sültemeyer and Rinast 1996; Ritchie 1987; Ritchie and Gibson 1987) due to their neutral nature. However, the proportion of inorganic carbon in the form of CO_2 and that of ammonia in the form of NH_3 are generally much lower than their ionized forms ($HCO_3^-/CO_3^=$ and NH_4^+ respectively) in the range of pH values where most macroalgae grow. For ionic forms, facilitated transport is necessary; in many cases, this involves energy-demanding mechanisms. However, this does not mean that facilitated transport mechanisms involve a lesser cost-effective cell; on the contrary, these mechanisms allow for the optimization of resources being invested. As an example, Raven et al. (2008) made a theoretical calculation on the transport and assimilation costs of nonfacilitated vs. facilitated mechanisms for N in the form of NH_4^+. In the case of the passive entry of NH_4^+, it requires the use of 560 times the N and NADPH to synthesize the relevant proteins, and 1.61 times the ATP to make the proteins and in running the transport and assimilation processes than in the case of facilitated uptake and assimilation of NH_4^+. These outcomes clearly show an optimized input of resources (N and energy) in achieving the outcome of a given rate of NH_4^+ assimilation in the case of a very low external concentration of NH_4^+. However, for some seaweeds, the relationship between uptake rate and concentration is a combination of a hyperbolic component due to active uptake and a linear diffusive component (Taylor and Rees 1998). These authors showed that seaweeds from New Zealand have lower ammonium uptake rates than their northern hemisphere counterparts, and suggested that uptake was due largely to passive diffusion of NH_3.

4.2.3 N vs. P Limitation

Under conditions of coastal eutrophication (see also Chap. 21 by Teichberg), fast-growing, ephemeral macroalgae bloom at the expense of slow-growing, perennial macroalgae. As mentioned above, this change in community composition has been explained by a differential ability to exploit and utilize inorganic nitrogen among macroalgae with different growth strategies. It is generally assumed that inorganic N availability is the main control for macroalgal growth in temperate coastal areas (Nixon and Pilson 1983; Oviatt et al. 1995; Howarth et al. 2000); however, some coastal areas have been identified as phosphorus- rather than nitrogen-limited. In tropical latitudes, P limitation might be established as carbonate sediments derived from coral reefs may sequester phosphate (Lapointe et al. 1992; McGlathery et al. 1994; Lapointe and Bedford 2010; see also Chap. 16 by Mejia et al.), although other studies have shown exceptions to this situation (Larned 1998; Fong et al. 2001; Elser et al. 2007). Teichberg et al. (2010) made a global survey of the growth response of *Ulva* spp. to experimental N or P enrichment across temperate and tropical sites and found that N and P limitation of growth was linked directly to nutrient availability and not to geographic or latitudinal differences as had been previously suggested (Howarth 2008). Teichberg et al. (2010) indicated that it is likely that ambient N:P ratios may be useful to predict nutrient limitation in bloom-forming species, despite the variability in the growth responses, uptake affinities, and tissue N and P storage capacities among macroalgal taxa (Fujita 1985; Pedersen and Borum 1996; Fong et al. 2003). Barile (2004) found that macroalgae with high uptake affinities for DIN (*Ulva lactuca*, *Chaetomorpha linum*, *U. intestinalis*, *Caulerpa* spp., and *Gracilaria tikvahiae*) were N-limited in subtropical coastal waters of east-central Florida, where water N:P was on average 8:1. In southeastern Brazil, macroalgal growth was P-limited where ambient N:P were greater than 16:1 (Lourenço et al. 2005). In contrast, in Waquoit Bay estuaries, where the water N:P ratio was approximately 3:1 during the growing season, *G. tikvahiae* (Teichberg et al. 2008) and *U. lactuca* (Teichberg et al. 2010) were N-limited. Lapointe and Bedford (2010) suggested that the blooms of the invasive *Caulerpa brachypus f. parvifolia* occurring at coral reefs off southeast Florida (USA) were P-limited due to high biomass N:P ratio despite relatively high ambient P.

Several studies have examined P-uptake kinetics in macroalgae (e.g., Wallentinus 1984; Hurd and Dring 1990; Gordillo et al. 2002; Runcie et al. 2004), some of them comparing growth-related P requirements to uptake kinetics and storage capacity (e.g., Björnsäter and Wheeler 1990; Lavery and McComb 1991). Pedersen et al. (2010) found that tissue P-concentrations, the balance between P-uptake and requirements, and the P-storage capacity varied systematically among the three groups of algae (i.e., algae with fast, intermediate, and slow growth).

4.2.4 Considering C as Just Another Nutrient

Traditionally, C has been considered as a special case when treated together with nutrients, since the term nutrient is reserved mainly for N and P (e.g., Rees 2003), and to a lesser extent S, Fe, Ca, and others, the latter set commonly being referred to as micronutrients. This might be due to the majority of nutrient studies being carried out in terrestrial plants, where C is taken from the air and the rest from soil by roots in most cases. C is usually considered to be at saturating concentrations. Although this is a pragmatic consideration for many studies on terrestrial plants nutrition, the uptake and assimilation dynamics of C in aquatic plants share many characteristics with other nutrients; i.e., it is essential for the cell, its utilization needs photosynthetic energy, there are specific transporters in the cell surface, it can be stored intracellularly and used later on when other restricting conditions ease, and its availability can limit growth.

The vast majority of algal primary production involves the C_3 pathway (the photosynthetic carbon reduction cycle or Calvin–Benson cycle) for DIC acquisition, fixing DIC directly via ribulose bisphosphate carboxylase oxygenase (Rubisco). However, Rubisco has a relatively low affinity for CO_2 and, for most species, it is consequently less than half saturated under current ambient CO_2 levels. The biochemical properties of Rubisco imply that for autotrophs dependent on diffusive CO_2 entry, the physiology of CO_2 assimilation is characterized by inherent inefficiencies, such as significant inhibition of CO_2 fixation by oxygen, high CO_2 compensation points, and low affinities for external CO_2.

An alternative source of inorganic carbon available is HCO_3^-. This is the most abundant form and can be converted to CO_2 to be used by Rubisco by means of both spontaneous or catalyzed dehydration. Spontaneous HCO_3^- dehydration kinetics in seawater are described in Johnson (1982). The rate of spontaneous CO_2 formation from HCO_3^- dehydration is clearly below the photosynthetic demand for most algae. Most algae meet their Ci demands by the operation of so-called carbon concentrating mechanisms (CCMs). The functional characteristics of these mechanisms have been reviewed by Giordano et al. (2005) (see also Chap. 19 by Roleda and Hurd and Chap. 2 by Gomez and Huovinen).

C and N Temporal Partition: As mentioned above, facilitated transport and assimilation mechanisms are cost-effective, optimizing molecules and energy invested in the process. This does not mean that the amount of energy invested in these mechanisms is a marginal proportion of that produced during photosynthesis (in addition to C assimilation in the Calvin–Benson cycle). On the contrary, they account for quite a significant amount of photosynthetic energy producing values for the photosynthetic quotient (PQ, number of C molecules fixed per O_2 evolved) lower than 1. In *Ulva rigida*, Gordillo et al. (2003) calculated that the amount of photosynthetically derived energy used in processes other than C fixation (operation of CCMs and other uptake and biosynthesis mechanisms) can account for nearly as much as 50%. When cultured at high pCO_2, CCMs were repressed and the proportion dropped to 28% despite the fact that in this species, the nitrate reductase activity (NR) was enhanced by CO_2 under nonlimiting NO_3^- supply. This suggests that in this species CCM could well account for >22% of the gross photosynthetic energy. Since CCM activity and C fixation need to be coupled, it is reasonable to question whether energy-demanding nutrient uptake and assimilation (other than C, mainly N) would benefit from any uncoupling mechanism.

Gordillo et al. (2002) suggested that in several brown algae, during the diel cycle, the reduction of nutrient uptake at the end of the dark period and the beginning of the light period may indicate a mechanism in which cellular energy is differentially distributed between nitrate and phosphate uptake mechanisms on one side and carbon uptake and fixation on the other, depending on the time of the day (Fig. 4.1). This strategy has been suggested by Falkowski (1975), Keller and Paerl (1980), Lean et al. (1982), and Turpin (1983) for some microalgal species. According to Gordillo et al. (2002), both the temporal partitioning of C and nutrients, and the ability to maintain nutrient uptake in darkness are consistent with a mechanism that reacts to the changing availability of these nutrients in an intertidal habitat. Gevaert et al. (2007) found in *Ulva* that rates of biosynthetic processes such as ammonium uptake are highest in the morning. Consistent with this hypothesis, the maximum rate of ammonium assimilation in *U. pertusa* peaked in the morning and coincided with low levels of the photosynthetic product sucrose, which peaked in the afternoon. There was a diurnal cycle in the rate of ammonium uptake and assimilation in light and dark, but the amplitude was much greater for assimilation than uptake. Moreover, these authors suggest that net ammonium assimilation only occurs during the day in *U. pertusa* and that two major roles for diurnal cycles are minimization of interspecific competition for resources and reduced metabolic costs. Further mechanistic models for C:N partition can be found in Flynn et al. (2001) and Wirtz and Pahlow (2010).

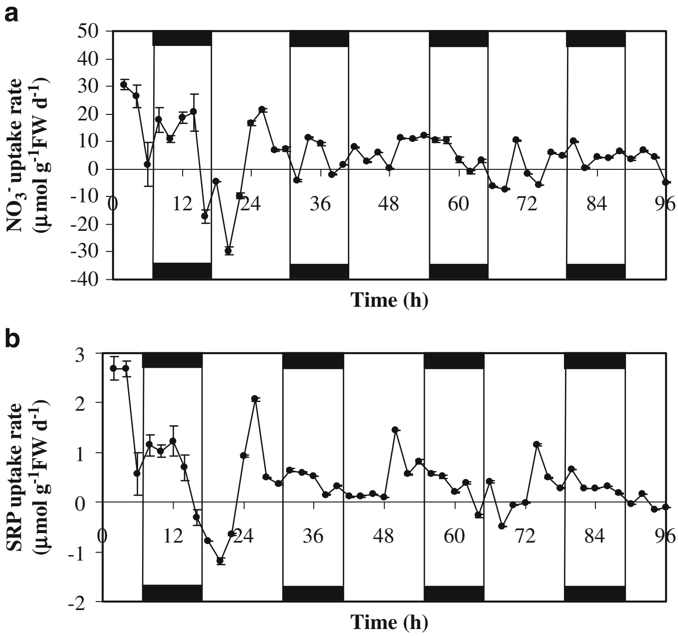

Fig. 4.1 Diel patterns of nitrate (**a**) and phosphate (**b**) uptake by *Fucus serratus*. *Black rectangles* represent the dark period [photoperiod 14:10 (L:D)]. Taken from Gordillo et al. (2002)

4.3 Uncoupling Uptake and Incorporation

Uptake and incorporation might be temporally and spatially uncoupled. In this context even storage in the vacuoles could be considered as spatial reallocation; however, it is more pragmatic to use the term "spatial uncoupling" when resources are reallocated in different parts of the thallus. In turn, storage in vacuoles is considered as a temporal uncoupling since nutrients can be immediately made available for assimilation and incorporation processes occurring in the cell whenever they are needed. According to Fujita (1985), differences in nutrient storage capacity between species may be important in structuring algal assemblages in environments with episodic N supply.

One of the most remarkable examples of temporal uncoupling is that found in polar kelps and kelp-like species (see also Chap. 13 by Wiencke and Amsler). The two polar coastal regions share some major characteristics, including low temperature and light regimes with complete darkness for months in winter and continuous sunlight for months in summer, as well as seasonal melting events of large ice masses. There are also key factors, however, differentiating both systems. In the Arctic, nutrients drop below detection limits during spring, and remain low until autumn mainly due to phytoplanktonic blooms occurring right after ice breakup (Aguilera et al. 2002). The Antarctic, however, is considered virtually unlimited by nutrients all year-round, and growth of algal species inhabiting the Antarctic is considered to be light-driven. This main difference in nutrient availability drives the internal regulation and strategies of light harvesting and nutrient assimilation. Although there are no kelps in the Antarctic, kelp-like *Himantothallus grandifolius* (Desmarestiales) is endemic to the Antarctic and dominates large coastal areas, but its growth is largely restricted to the ice-free months in spring (Drew and Hastings 1992; see also Chap. 13 by Wiencke and Amsler). On the other hand, the kelp *Laminaria solidungula*, endemic to the Arctic, stops its growth during N-depleted summer and accumulates carbon skeletons that are used for growth later in winter when N becomes available (Henley and Dunton 1995). According to Korb and Gerard (2000), *L. solidungula* can be considered a "storage specialist" for nitrogen assimilation. Its high $V_{\max}$ for nitrate uptake, coupled with low growth rates, allows Arctic plants to take advantage of seasonally elevated concentrations and accumulate large internal pools of nitrate and organic N-reserves. In the Antarctic, *H. grandifolius* does not accumulate nitrate, so that N-uptake characteristics are better adapted to optimize energy consumption rather than N-assimilation. Preferential use of NH_4^+ over NO_3^- displayed by *H. grandifolius* (but not by *L. solidungula*) would add evidence of an energy-saving strategy (Korb and Gerard 2000; see also Chap. 2 by Gómez and Huovinen, Chap. 13 by Wiencke and Amsler). It is then expected that these two different strategies will ultimately determine their ability to face a given environmental change.

Traditionally, it was thought that this seasonal growth pattern observed in Arctic kelps was a direct consequence of N availability (Chapman and Lindley 1980) as well as light availability (Henley and Dunton 1997). However, it has become apparent that, at least in some species, this pattern is under the control of an endogenous free-running circannual rhythm entrained by a critical minimum daylength in autumn (Lüning 1991; Schaffelke and Lüning 1994). This suggests that the addition of nitrate-N to summer N-limited kelps would have only a marginal effect on growth and biochemical composition, presumably due to the prevailing internal clock (Henley and Dunton 1997). Gordillo et al. (2006) confirmed that the effects of nutrient enrichment on biomass composition play only a marginal role in a number of species from Kongsfjord (Svalbard). When thalli of 21 species were collected in summer and incubated for 2 days under nitrate and phosphate enrichment, the C:N ratio was only affected by 7% on average. Lack of N accumulation and enhanced photosynthetic ability is in agreement with the internal clock prevailing over external nutrient conditions, which in summer would promote active photosynthesis over nutrient use.

4.4 Different Ways of N Utilization

Sources of N for macroalgal growth are mostly in the form of nitrate and ammonium, and the metabolism of inorganic N by algae is known to be regulated by both N forms (Solomonson and Barber 1990). Furthermore, different species show different preferences and dynamics for each N form. The use of nitrate has a clear advantage over ammonium since it can be stored in a vacuole with a concentration factor (internal:external) of $>$1,000 (e.g., Gordillo et al. 2002), while high concentrations of ammonium are toxic, acting as an uncoupler (Krogmann et al. 1959). On the other hand, ammonium has an energetic advantage over nitrate (but this is a minor issue when light is saturating). As a cation, less energy is required for transport, and it can be immediately used for amino acid synthesis via glutamine synthetase/ glutamine–oxoglutarate aminotransferase (GS/GOGAT), while nitrate must be reduced to nitrite by the highly regulated enzyme nitrate reductase, and then nitrite must be further reduced to ammonium by the nitrite reductase, investing eight electrons per NO_3^- molecule being reduced to NH_4^+ overall (e.g., Raven 1984).

For most algae, ammonium is the preferred inorganic N form. According to Rees (2003), ammonium uptake is more efficient than nitrate uptake in macroalgae. In addition, the presence of ammonium can suppress the uptake and assimilation of less reduced forms of N, mainly nitrate, in phytoplankton (Dortch 1990) and macroalgae (DeBoer 1981; Harrison et al. 1986; Naldi and Wheeler 2002). Elevated ammonium concentrations can also result in a decline in the activity of the primary nitrate-assimilating enzyme, nitrate reductase (NR) in microalgae (Berges et al. 1995; Vergara et al. 1998), and in a brown macroalga, *Giffordia mitchellae* (Weidner and Kiefer 1981). Ammonium was taken up at a higher rate than nitrate when presented alone (Lotze and Schramm 2000; Nishihara et al. 2005) or simultaneously (Naldi and Wheeler 2002; Cohen and Fong 2004).

4.4.1 Seaweed Diversity Linked to Nutrient Source

Ammonium is primarily associated with local scale regeneration, whereas nitrate availability is predominantly determined by oceanographic processes in the adjacent nearshore and/or runoff from land. The physiological mechanisms by which each form is used differ substantially, and seaweeds with different morphologies, physiological capabilities, and life-history strategies might differ in their abilities to utilize nitrate vs. ammonium (e.g., Naldi and Wheeler 1999). However, Bracken and Stachowicz (2006) found that, in diverse seaweeds assemblages, the uptake of either nitrate or ammonium alone was equal to the average of the component monocultures, but when nitrate and ammonium were available simultaneously, total N uptake by the assemblage was 22% higher than the average from monocultures because different species were complementary in the use of the nitrogen forms. These results provide a mechanistic link between N use and the diversity of primary producers in marine ecosystems. Previously, Bracken and Nielsen (2004) found that in nitrate-exhausted intertidal pools, slow-growing species tolerant to low nitrogen availability were joined by fast-growing species with higher nitrogen requirements due to increased ammonium loadings coming from macroinvertebrates. A fourfold increase in the ammonium loading rate was associated with a doubling in the number of macroalgal species.

Other factors such as herbivory greatly influence diversity. However, niche partitioning by the differential N use can reduce competition and lead to greater N fluxes into the intertidal food web. The effect of resource-based niche partitioning on diversity has been also suggested in terrestrial ecosystems (McKane et al. 2002). The nutritional status of aquatic primary producers has been found to determine the efficiency of energy transfer through food chains (the so-called food chain efficiency, FCE), with the carryover effects of algal quality across trophic levels (Dickman et al. 2008).

4.4.2 *Slow-Growing vs. Fast-Growing Species*

Aquatic plant communities are formed by a number of species representing various growth strategies and life forms, and the contribution of the different plant types to total autotrophic biomass and production is regulated by several factors that influence growth and loss processes. The distribution of macroalgae along nutrient gradients is typically characterized by slow-growing species in nutrient-poor regions or seasons, while fast-growing, ephemeral species dominate under nutrient-rich conditions (e.g., Kautsky et al. 1986; Taylor et al. 1995; Borum and Sand-Jensen 1996; see also Chap. 21 by Teichberg). The association between high nutrient availability and increased dominance of ephemeral macroalgae suggests that fast-growing species require high nutrient inputs to sustain growth, while large, slow-growing species are better adapted to nutrient-poor conditions. In support of this idea, Pedersen and Borum (1996) demonstrated that ephemeral macroalgae suffered from N limitation during longer periods of low N availability in summer than did slow-growing species. The observed variation in N limitation among algae of different growth strategy could partly be explained by species-specific differences in N requirements and storage capacity (Pedersen and Borum 1997). As an example, Lartigue and Sherman (2006) found that, under fluctuating NO_3^- discharges to an estuary, total N in the nitrophillic fast-growing *Ulva lingulata* ranged from 2.6% to 6.4% dry weight, while the slower growing *Gelidium pusillum* showed no significant variation in total N content (3.8–4.1% dw). Additionally, Pedersen and Borum (1996) also indicated that, compared to ephemeral species, slow-growing macroalgae were better able to meet their N requirements by exploiting low external N concentrations. Other studies have associated a higher position in the intertidal with higher internal nitrate pools (Phillips and Hurd 2003), higher NR activities (Murthy et al. 1986), and elevated nutrient uptake capacity, which may compensate for periods of emersion (Hurd and Dring 1990; Phillips and Hurd 2004). However, this association is not always valid, and contrasting results have also been found (Young et al. 2009).

4.5 Use of Isotope Discrimination

The stable nitrogen isotope ^{15}N discrimination (∂^{15}N) has been frequently used to determine nitrogen sources in ecosystem studies (Peterson and Fry 1987; McKinney et al. 2001; Cole et al. 2004; Lapointe 2004). The underlying assumptions are that the ∂^{15}N of sources are known and that primary producers take up ^{15}N in proportion to availability in a predictable manner (Cifuentes et al. 1988). The natural abundance of ^{15}N in many sources has been measured, including fertilizer (0‰), sewage (10‰–20‰), soil (5‰), and rainfall (−3‰ to −5‰; Heaton 1986). Groundwater, depending on the amount of microbial processing that selects for ^{14}N and leaves the remaining N in ^{15}N, can exceed 30‰ (Page 1995). Cohen and Fong (2005) showed that *Ulva intestinalis* did not differentially select ^{14}N over ^{15}N in a range of N concentrations and isotopes proportions. Rather, the species took up ^{14}N and ^{15}N in direct proportion to the amount in the source, suggesting that this alga may be useful for determining N sources in estuaries. However, uptake preference for ^{15}N-ammonium rather than ^{15}N-nitrate can result in differences in tissue ∂^{15}N that may confound its use as an indicator. For example, if ammonium from sewage with a low ∂^{15}N and nitrate from groundwater with a high ∂^{15}N co-occur in an estuary and the algae take up more ammonium, then it will appear that the sewage is a more important source relative to groundwater even though it may not be. Teichberg et al. (2010) showed that ∂^{15}N of macroalgae is generally heavier where DIN concentrations are higher due to increased N loads associated with wastewater rather than other N sources in many coastal waters. Fast-growing algae, such as *Ulva* spp. and *Gracilaria* spp., are better at reflecting the ∂^{15}N values of the N source in a shorter period of time (Aguiar et al. 2003; Teichberg et al. 2008), but this might not be the case when examining slower growing algae such as *Fucus vesiculosus* (Deutsch and Voss 2006).

4.6 Aquaculture

Seaweeds have an essential role for maintenance and expansion of sustainable marine aquaculture (Chopin et al. 2001; Neori 2008; see also Chap. 22 by Buchholz et al.). The integration of seaweeds to marine animal cultures has long been recognized as the most promising approach to reduce the excess nutrients released by aquaculture activity, due to the high nutrient uptake efficiency of macroalgae, their fast growth rates, and economical and practical aspects of their cultivation (Vandermeulen and Gordin 1990; Shpigel et al. 1993; Chopin et al. 2001; Hernández et al. 2006; Lüning and Pang 2003; Neori et al. 2004). Research and development of integrated mariculture, recently known as integrated multi-trophic aquaculture (IMTA), has advanced over the last 20 years (Neori et al. 2004), although it still needs to be implemented at a larger scale by the modern global industry (Hernández et al. 2002). Some of the state-of-art seaweed-based integrated aquaculture has now been focused on the cultivation of high-value seaweed species which have not been previously used in integrated systems, and on improving tank-culture success for seaweed yields and for reduction of undesirable effects of intensive fish mariculture (e.g., Mata et al. 2006; Hernández et al. 2006; Flower and Neori 2008).

The majority of the research on integrated mariculture is based on the integration of biofiltering seaweed and fish aquaculture. There are also studies focussed on the integration of seaweed and shrimp culture (e.g., Jones et al. 2001; Sato et al. 2006a, b; Lombardi et al. 2006) and human sewage (Gordillo et al. 2002). Thus, treatment with macroalgae has now become an alternative to earlier adoptions of microalgae, but care must be taken when extrapolating pilot plant results to a larger scale. The factors for considering the advantages of using a given species over others should include that they are abundant in the system during the whole year and are easier to maintain in long-term cultures. For example, for human sewage treatment Gordillo et al. (2002) showed that the intertidal species *Fucus vesiculosus* and *F. serratus* have the ability to adapt to high nutrient concentrations and low salinity and are, therefore, suitable candidates for wastewater treatment, while the subtidal *Laminaria digitata* would be a less suitable species since it did not stand long periods under reduced salinity despite its N accumulating ability.

4.6.1 Nutrient Uptake at High Concentrations

Frequently, when a given resource is available at concentrations well above the $K_{0.5}$ of the high affinity uptake mechanism, a second uptake mechanism can be observed showing uptake rates above the $V_{\max}$ of the former (e.g., Fujita 1985; Gordillo et al. 2002, Fig. 4.2). Nonsaturating and biphasic uptake kinetics have been observed in coastal phytoplankton assemblages, which normally bloom under conditions of high nutrient fluxes and turbulent mixing and are considered to be mechanisms of adaptation to such environments (Collos et al. 1997; Lomas and Glibert 1999). Furthermore, nonsaturating nutrient uptake kinetics have been reported for several macroalgae species by Wallentinus (1984) and Fujita (1985). Biphasic kinetics was observed in the red alga *Gracilaria gaditana* when inorganic carbon uptake was investigated at high CO_2 levels (Andría et al. 1999). Gordillo et al. (2002) evidenced that the onset of a second mechanism in *Fucus serratus* dealing with high external phosphate is apparently different from the high affinity one operating at low concentrations (Fig. 4.2). These adaptations would make the N:P ratio for uptake drop from values around 30 at relatively subsaturating nutrient levels to values more in accordance with internal inorganic N:P ratios observed when internal pools are saturated. Since common assay concentrations are rarely above 30 μM for both N and P, Lomas and Glibert (1999) have suggested, from their results with phytoplankton, that more nonsaturating and biphasic uptake kinetics may be found in algae of coastal areas if researchers use a wider range of concentrations in their assays.

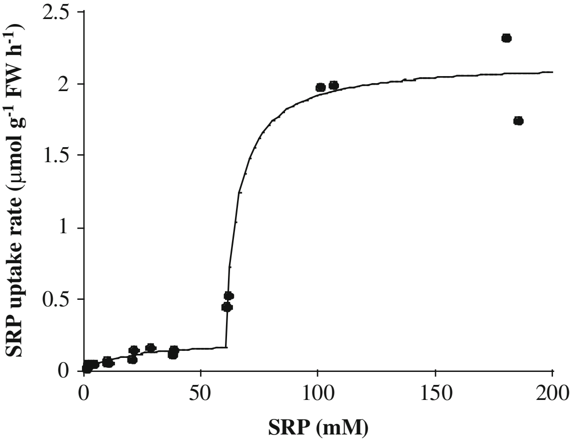

Fig. 4.2 Phosphate uptake rate as a function of external phosphate concentration (soluble reactive phosphate, SRP), fitted to two different Michaelis–Menten equations. Taken from Gordillo et al. (2002)

4.7 Conclusions

The coastal environments are characterized by strong and rapid changes in abiotic factors, among which nutrients load play a key role. Evolution has provided macroalgae with different mechanisms that allow for optimization of resources available. Regarding nutrient acquisition, this implies not only the enzymes for uptake and assimilation. A wide variety of combinations are displayed by the different species. Some are storage specialists; others are more restricted to external availability. Periods of intense nutrient uptake do not necessarily mean faster growth, and during the course of the day, algae can switch their photosynthetic energy investment from C to N and P acquisition. Overall, the major output is that these different mechanisms for the different species coexist at the same time in the same community, and this strategy partitioning allows a more effective resource use, and an increased availability of nutrients to the rest of the food web.

Future research is needed to quantify the benefits of the coexistence of mixed strategies, and how are these combinations going to be affected by the modification of other abiotic factors such as temperature and salinity, the latter being particularly relevant for threatened ice-driven ecosystems such as the Arctic and the Antarctic. Many ongoing studies are focusing on the modification of geographical distribution boundaries for different ecologically relevant species, commonly being related to changes in water temperature and currents pattern. However, the result might also depend on the ability of a given species to deal with a new nutrient regime. The incorporation of this approach to geographically relevant studies will add knowledge on the mechanisms determining the distribution of species.

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Chapter 5
Seaweed Acclimation to Salinity and Desiccation Stress

Ulf Karsten

Dedicated to my mentor Professor Dr. Gunter O. Kirst on the occasion of his 70th birthday.

5.1 Variability of Salinity in Seaweed Habitats

Salinity is a technical term in marine sciences and represents the sum of all dissolved salts of a defined body of water. Therefore, marine biologists for a long time used the expression *promille* (‰) or *parts per thousands* (ppt) to describe salinity concentration. In contrast, since 1978 oceanographers defined salinity in the Practical Salinity Scale as dimensionless Practical Salinity Units (PSU) which is the conductivity ratio of a seawater sample to a standard KCl solution. In October 2010, the Intergovernmental Oceanographic Commission (IOC), International Association for the Physical Sciences of the Oceans (IAPSO), and the Scientific Committee on Oceanic Research (SCOR) jointly adopted a new standard for the calculation of the thermodynamic properties of seawater. This new standard, called TEOS-10, uses Absolute Salinity S_A (mass fraction of salt in seawater) to describe the salt content of seawater. Ocean salinities now have units of g dissolved salts kg^{-1} water (http://www.teos-10.org; Wright et al. 2010). Therefore, all salinities throughout the text are expressed as Absolute Salinity S_A.

The chemical composition of the dissolved salts is relatively constant throughout the open oceans due to intensive mixing, and it varies only between 33 and 37 S_A, gradually decreasing from the subtropics toward the tropics and polar seas. In contrast, salinity strongly varies in nearshore waters and estuaries where river freshwater mixes with marine water bodies. Here horizontal and vertical gradients between 0 and 33 S_A can be measured. The degree of salt dilution in estuaries

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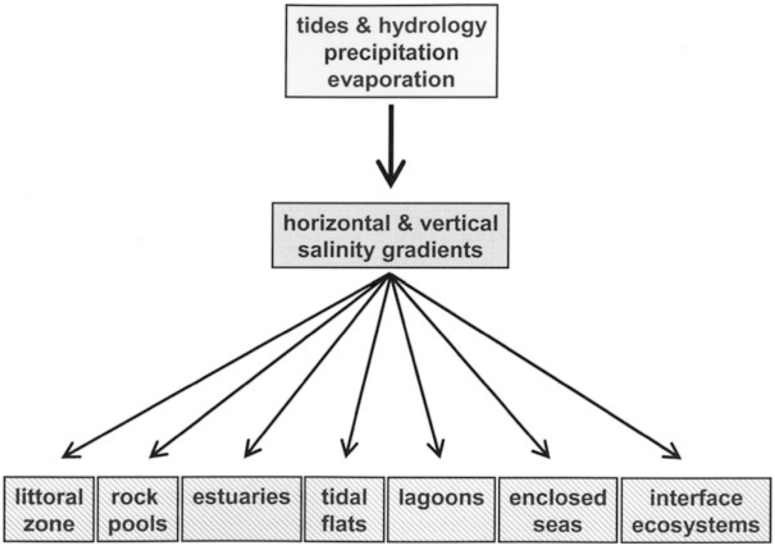

Fig. 5.1 Illustration of the abiotic factors influencing salt concentration resulting in horizontal and vertical salinity gradients in various aquatic systems

largely depends on the rate and volume of freshwater runoff, and can be dramatic. The water of the Amazon, for example, can be recognized at the surface of the open Atlantic Ocean for approximately 300 km (Ryther et al. 1967). Since the geochemistry of the river's catchment area is typically highly variable as well, it strongly affects besides the salt concentration also the salt composition in estuaries. In addition, tidal flows, hydrological conditions, wind, precipitation, and evaporation strongly influence salt concentration of the respective water bodies (Fig. 5.1). Consequently, salinity is typically a local rather than a global parameter and can be highly variable in coastal regions.

Since most seaweeds are sessile organisms that preferentially grow attached to hard substrata such as rocks, gravel, or as epiphytes on salt marsh plants, on mangroves, and on mussel colonies, they are mainly confronted with salinity fluctuations and desiccation when exposed at low tides. At lowest water levels, hyposaline conditions may be present due to the mixing of seawater with rain, snow, or melt water, while hypersaline stress may occur due to evaporation during high insolation in summer or freezing-out of freshwater in winter. In addition, in estuaries and fjords which often exhibit extensive seaweed communities (Schramm and Nienhuis 1996), rivers or freshwater runoff mix with seawater resulting in diurnally and seasonally fluctuating salinity gradients. In Arctic waters, seaweed species can be strongly affected by melt water influx and calving glaciers (Hanelt et al. 2001; Karsten et al. 2003a).

Most seaweeds such as kelps inhabit the sublittoral which is characterized by quite stable environmental factors, and hence these more deepwater plants only rarely experience salinity and desiccation stress. One of these occasions, however, is spring low tides where sublittoral seaweed species may be exposed for some time to salinity changes and desiccation (Lüning 1990). Besides the intertidal zone and estuaries, there are other habitats occupied by seaweeds which are affected by salinity changes or gradients (Fig. 5.1). Rock pools at low tide often exhibit strong salinity fluctuations due to precipitation or evaporation. Seaweeds living on tidal flats (e.g., on mussel beds) or in interface ecosystems (salt marshes, mangroves) are regularly affected by the tidal flows and hence to a combination of salinity and desiccation stress. In mangroves epiphytic red algae exposed to the prop roots can be observed completely covered with salt crystals. Semi-enclosed seas with only small connections to the open oceans mostly exhibit strong horizontal salinity gradients or hypersaline conditions depending on the hydrology of the catchment area and precipitation. The best studied semi-enclosed system is the Baltic Sea with its strong, but stable horizontal salinity gradient from almost freshwater conditions in the Northeast to brackish/marine conditions in the western part. Since the largest part of the Baltic Sea shows a salinity between 4 and 7 S_A only, biodiversity of the aquatic flora (incl. seaweeds) and fauna is generally strongly reduced, because this salinity range (ß-mesohalinum 5–10 S_A) is too low for marine species and too high for freshwater organisms (Remane 1940). In warm-temperate to subtropical coastal regions such as South Australia, lagoons are typical shallow water systems that are separated from the open ocean by some form of barrier (e.g., sand spit) resulting in often hypersaline conditions because of the high prevailing evaporation. A typical example is the Coorong lagoon in South Australia with salinities >100 S_A, where high abundances of charophyte algae can occur (Bisson and Kirst 1983). Marine and brackish waters are consequently almost infinitely variable in the amplitude and frequency of their saline changes, which of course has various consequences for the physiological performance of seaweeds.

5.2 Effects of Salinity Stress and Desiccation on the Physiology of Seaweeds

Since decades, the effects of salinity and desiccation on the ecophysiological performance of seaweeds have been described to outline the species-specific width of tolerance, i.e., upper and lower limits for survival, as well as mechanisms for acclimation (Kirst 1990 and references therein). Nevertheless, both salinity stress and desiccation reflect two different forms of water deprivation. While under salt stress conditions, seaweed cells are still in full contact to liquid water of diminished water potential, desiccation leads to strong cellular dehydration. Typical physiological parameters which have been studied under such stress conditions include rate of survival, growth, photosynthesis, respiration, and reproduction.

5.2.1 Rate of Survival

The rate of survival can be easily estimated by following seaweed growth or photosynthesis activity under defined stress conditions, or using classical vital staining techniques for individual cells such as Evans Blue (Russell 1985; Thomas and Kirst 1991). Only dead cells with damaged membranes will take up this stain and hence appear blue under the microscope. These days a range of commercially available fluorescence dyes such as the so-called Live–Dead kits are available which in combination with an epifluorescence microscope allow the evaluation and visualization of even smallest damages on membrane integrity.

The available data on cell viability in relation to salinity indicate that members of eulittoral green algal genera such as *Ulva* (incl. *Enteromorpha*), *Acrosiphonia*, *UIothrix, Cladophora*, and *Prasiola* are generally much less affected than sublittoral red and brown seaweeds (Russell 1985, 1987, Kain and Norton 1990; Thomas and Kirst 1991; Karsten et al. 1991a). While even under triple seawater concentration >75% of green algal cells remain intact, mortality in sublittoral brown algae such as *Phaeurus antarcticus* increased to almost 100% (Karsten et al. 1991a). This rather euryhaline feature of eulittoral green seaweeds may be considered as important environmental factor for controlling vertical species zonation on the shore (Russell 1987).

5.2.2 Growth

From an ecological perspective, growth represents the most relevant physiological process to describe the performance of seaweeds in their respective habitat because it optimally integrates all positive and negative environmental effects on the organism and hence reflects the acclimation potential (Gustavs et al. 2009). A careful analysis of growth patterns allows the evaluation of salinity tolerance limits, growth optima, and acclimation abilities of individual seaweed species, and, thus facilitates the interpretation of natural distributions. Knowledge of physiological limits is necessary to estimate and understand distribution limits within an unknown community, i.e., in a competitive situation. Additionally, the shape of the growth rate curve in dependence of any abiotic factor characterizes a seaweed species as steno- or euryoecious, or in case of salinity as steno- or euryhaline, which definitively affects its competitive strength.

Until now, numerous ecophysiological studies have been undertaken on the salinity effects on growth in seaweeds (Jacob et al. 1991; Karsten et al. 1991a, 1993b, 1994, 1996b; Karsten and West 1993; Kirst 1990 and references therein, Thomas and Kirst 1991). All these papers clearly indicate that eulittoral seaweeds from polar to tropical regions grow between low salinities (5–10 S_A) and double seawater concentration (66–68 S_A), in most cases with conspicuous optima under normal seawater conditions. The supralittoral *Prasiola crispa* ssp. *antarctica* even grows between 0.3 and 105 S_A (Jacob et al. 1991). In contrast to the generally broad salinity tolerance of upper-shore seaweeds, those from the sublittoral usually exhibit the narrowest tolerance limits (Russell 1987). Salinities commonly encountered in areas of abundance are most favorable for growth (Bird et al. 1979; Bird and McLachlan 1986). This is well reflected in the growth pattern of the green alga *Ulva pertusa* from an eelgrass bed in a semi-protected bay at the southwest coast of Korea (Choi et al. 2010). *Ulva pertusa* exhibited optimum growth at 20 S_A, a situation encountered in the field during the rainy season when this species often forms blooms in eelgrass beds. Growth under hyposaline conditions, i.e., in aquatic systems such as estuaries or the eastern part of the Baltic Sea, may be governed by the availability of certain inorganic ions which increase the lower tolerance limits of seaweeds. In this context, the presence of Ca^{2+} plays an essential role in cell signaling, as structural component of seaweed cell walls and membranes, and as cation to balance organic anions in the plant vacuole (Kauss 1987; Tazawa et al. 1987; Verret et al. 2010). Whole seaweed thalli have been reported to exhibit differential salinity tolerances. Particularly young apical growing parts of species of the genera *Cladophora*, *Ceramium*, *Phycodrys*, and *Plumaria* are more sensitive to hyposaline conditions than older, basal parts (Russell 1987). Kirst (1990) speculated that this observation is a secondary effect of Ca^{2+} availability, as particularly fast-growing cells depend on this cation, for example, for cell wall formation.

If not only growth but also survival is considered, most seaweeds show a remarkable physiological potential. While the red alga *Porphyra umbilicalis* exhibits optimum growth between 7 and 52 S_A, it survived without cell division even in sixfold fully marine salinities for 2 weeks (Wiencke and Läuchli 1980). Similar observations have been reported in the studies of elongation growth in the siphonous green alga *Valonia macrophysa* (Gutknecht et al. 1978). Near the limits of salinity tolerance, growth of most studied seaweeds is typically strongly reduced or even completely inhibited in order to funnel all available metabolic energy into the process of osmotic adjustment, which guarantees survival under fluctuating salinities. Besides these energetic considerations, high inorganic ion concentrations under salt stress conditions exert negative, i.e., inhibiting effects on seaweed growth. This is reflected in conspicuous changes in size and morphology of seaweeds under long-term salt stress (Russell 1987).

If additional environmental factors that greatly affect the growth rate of seaweeds as well are included in the investigation of the growth–salinity relationship (e.g., radiation (UV), temperature, etc.), the emerging picture becomes very complex. Therefore, only a few macroalgal species have been investigated in this respect, such as the green algae *Cladophora glomerata* and *C. rupestris* (Thomas et al. 1988), the red alga *Polysiphonia lanosa* (Reed 1983), or the kelp species *Laminaria groenlandica* and S*accharina latissima* (Druehl 1967). Low salinity may be compromised by temperature as shown for North Pacific *L. groenlandica* which cannot tolerate the combination of low salinity and high temperature conditions encountered in areas subjected to snow-melt runoff, whereas *S. latissima* can. Both species, however, do well in areas subjected to winter rain runoff where cold conditions prevail (Druehl 1967). All available data indicate that growth of seaweeds primarily depends on radiation and temperature conditions, and the more these environmental factors approach species-specific optimum requirements, the broader is the salinity range tolerated. In addition, if seaweeds are exposed to desiccation during low tides, growth is completely inhibited. The physiological strategy is to cope with and survive this stress condition by maximum reduction of all metabolic activities.

5.2.3 Photosynthesis and Respiration

Besides growth, photosynthesis and respiration are two central physiological processes in seaweeds which are strongly affected by salinity changes (Kirst 1990). Under extreme hypo- or hypersaline conditions, photosynthesis and respiration are typically completely inhibited and in many cases confirm the growth–salinity relationships described above. Whether salinity stress is extreme depends on the habitat and vertical zonation of the respective seaweed species, because sublittoral taxa are generally much more sensitive and hence stenohaline than their eulittoral, mainly euryhaline, counterparts (Russell 1987). A relatively salt-insensitive photosynthesis and respiration seem to be a prerequisite for the successful occupation of the eulittoral habitat and may ensure long-term survival and reproduction under large amplitudes of salinity in combination with other environmental factors (Gessner and Schramm 1971). A similar relation regarding photosynthesis as a function of desiccation was reported in various seaweeds from different tidal heights (Wiltens et al. 1978). In addition, photosynthesis and respiration exhibit different responses under a range of salinities as documented for a set of eulittoral green algae from Antarctica (Karsten et al. 1991a; see also Chap. 13 by Wiencke and Amsler). While most investigated species showed optimum photosynthesis at 34 S_A and decreasing rates between 7 and 17 S_A as well as between 51 and 68 S_A, respiration was much less affected. Similarly, under desiccation photosynthesis of seaweeds is much more affected than respiration (Wiltens et al. 1978).

The photosynthetic and respiratory responses following exposure to moderate and high changes in salinity are inconsistent among seaweeds. Frequently, a transient stimulation of respiration and a stimulatory or inhibitory effect on photosynthesis have been observed (Kirst 1990). The time required for a more or less complete recovery is species specific and lasted for several hours to days for seaweeds (Kirst 1990).

Using chlorophyll fluorescence kinetics, the underlying processes leading to salt-induced inhibition of photosynthesis were studied in various eulittoral green and red alga (*Prasiola*, *Ulva*, *Porphyra*) (Wiltens et al. 1978; Fork and Öquist 1981; Satoh et al. 1983; Smith et al. 1986). These investigations were aimed primarily at measuring the effects of desiccation on photosynthesis. The two stresses (increasing salinity and desiccation) are comparable since they result in a reduction of the cellular water potential. During desiccation, however, cellular ionic concentrations increase and the ion ratios remain constant. In contrast, during salinity stress algal cells may not only increase ionic concentrations but also undergo changes in ion ratios owing to selective uptake. This has to be taken into account when comparing the results obtained with species under salt or desiccation stress.

The primary photosynthetic mechanism is affected at the electron transport stage between PS I and PS II. The sensitive site in *Porphyra* and *Ulva* species is most likely between plastoquinone and P 700 (Wiltens et al. 1978). In *Porphyra perforata* there seem to be at least three sites in the photosynthetic apparatus that are inhibited by high salinity, namely the photoactivation of electron flow on the reducing side of PS I, the electron flow on the water side of PS II and the transfer of light energy between the pigment complexes (Satoh et al. 1983). These authors concluded that a free electron flow at all three sites is essential to avoid photodamage through chronic photoinhibition, which will occur if only one site is blocked because of, e.g., the accumulation of highly reactive oxygen species(ROS; see also Chap. 6 by Bischof and Rautenberger).

More recent data on cyanobacteria indicate a salt-induced inactivation of both oxygen evolution in PSII and electron transport in PSI (Allakhverdiev and Murata 2008). The site of inactivation is the electron-donating side of PSII, i.e., the oxygen-evolving machinery, due to the influx of uncontrolled Na^+ and Cl^- ions with resultant dissociation of extrinsic proteins from photosystems (Allakhverdiev and Murata 2008).

5.3 Processes of Osmotic Acclimation

Hypersaline conditions in the external medium affect seaweeds in two ways: first, the water potential is strongly reduced leading to dehydration of cells, and secondly, high concentrations of some inorganic ions exert toxic effects on cellular metabolism. Similarly, desiccation stress will also result in strong dehydration of cells. Since both hypersalinity and desiccation affect the internal osmotic potential, the acclimation responses of seaweeds are comparable.

Water is taken up in all living cells by osmosis, which is driven by the water potential gradient, i.e., only if the intracellular water potential is lower than in the external medium there is a water influx. Consequently, marine seaweeds have to create an internal osmotic potential higher than that of seawater to gain and retain constant water content of the cells, which is necessary to maintain turgor as the driving force for growth. Seaweeds typically respond to external salinity changes with osmotic acclimation processes which involve the control of cytoplasmic and vacuolar concentrations of osmotically active compounds (Kirst 1990). Therefore, osmotic acclimation is a fundamental mechanism of salinity tolerance of these plants that conserves the stability of the intracellular milieu (homeostasis), and it is essential for maintaining an efficient functional state in the cells (Kirst 1990). Most seaweeds use inorganic ions and small organic osmolytes to create the internal osmotic potential.

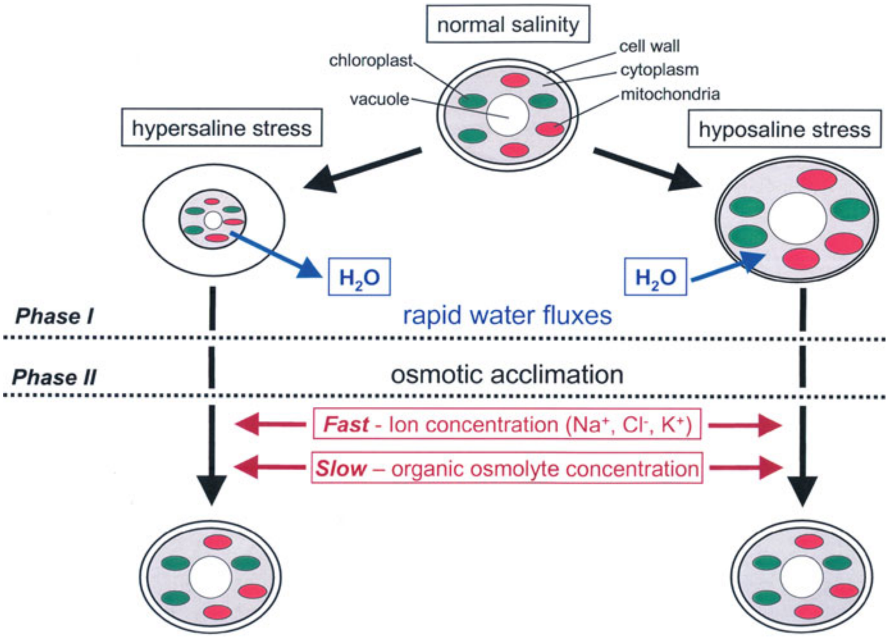

Fig. 5.2 Schematic summary of the processes of osmotic acclimation in seaweeds after hypersaline and hyposaline stress leading to a new steady state

The response of seaweeds to salinity changes is a well-regulated biphasic process. Phase I is characterized by rapid changes in turgor pressure caused by massive water fluxes in or out of the organism following the osmotic gradient. Phase II represents the process of osmotic acclimation, i.e., adjustment of the intracellular concentrations of the osmotically active inorganic ions and organic osmolytes until a new steady state is achieved (Fig. 5.2). Both phases are part of a feedback loop that comprises the osmotic acclimation.

The water fluxes during phase I are rapid processes with half times in seaweeds lasting from minutes to hours (Zimmermann and Steudle 1978), resulting in water influx under hyposaline conditions or water efflux during hypersaline stress, both of which mitigate at least transiently the osmotic stress (Fig. 5.2). Most importantly, these processes follow passive "osmometer" behavior, and depend on physico-chemical properties of the cell-wall membrane complex such as the hydraulic conductivity (water permeability, water channels). So far it has been assumed that all phase I processes are not under metabolic control (Kirst 1990), but since the discovery of the so-called aquaporins as membrane-located water channels it seems that cells can control their water content (Törnroth-Horsefield et al. 2006). These channels are widely distributed in all kingdoms of life. They form tetramers in the plasmalemma, and facilitate the transport of water through the lipophilic membrane. Probably, many water channels at the cytoplasmic membrane open for short time during salt stress, and not only water but also small water-soluble solutes are taken up or lost during phase I.

In contrast to the phase I, phase II is a rather slow process in seaweeds lasting from several hours up to 2–3 days (Kirst 1990, Karsten et al. 1996b). As a result, the internal osmotic potential becomes adjusted by changing the concentrations of ions and organic osmolytes to restore the original turgor pressure. These processes are under direct metabolic control.

5.3.1 Inorganic Ions

To adjust inorganic ion concentrations to homeostatic conditions, ions are actively extruded under hypersaline conditions but must be imported under hyposaline stress. The main ions involved in osmotic acclimation are K^+, Na^+, Cl^- and to a lesser extent sulfate, nitrate, or phosphate. The ionic composition of algal cells and in particular of their vacuoles varies widely depending on cellular number and volume of vacuoles (Kirst 1990). In most seaweeds, the Cl^- concentration usually follows the fluctuation in salinity. With respect to the Na^+ content, particularly siphonous green algae such as members of the genera *Caulerpa*, *Halimeda* or *Bryopsis* with their huge vacuolar system accumulate this cation. In contrast, other seaweeds with small vacuoles and high cytoplasmic fraction prefer to accumulate K^+ under salinity stress (Kirst 1990). In contrast to the toxic properties of Na^+ (and Cl^-), K^+ is fully compatible to metabolic activities, although an explanation for this fact is still missing (Maathuis and Amtmann 1999). Both cations exhibit similar physico-chemical properties, as the smaller Na^+ together with its rather large hydration shell mimics the size of K^+. Consequently, uptake systems for K^+ have difficulties discriminating between both ions, and high external Na^+ amounts may result in K^+ deficiency. Inside the cell, Na^+ can compete for K^+-binding sites of proteins, which contribute to their stabilization, resulting in the inhibition of K^+-dependent metabolic processes (Hagemann 2011). Therefore, all organisms tend to ensure a defined usually high K^+/Na^+ ratio in the cytoplasm (Maathuis and Amtmann 1999).

During osmotic adjustment, the changes in and control of ion composition are achieved by regulating the activity of specific transport systems, which are particularly well studied in cyanobacteria (Hagemann 2011) and probably act also in seaweeds. Ion concentrations in algae are mainly regulated by ion-selective carriers driven by the membrane potential (Gimmler 2000). In addition, facilitated diffusion via ion-selective channels may play a role during rapid changes and recovery of ionic composition (Kirst 1990).

The generally low cytoplasmic Na^+ concentrations observed in most seaweeds clearly indicate that active sodium ion export mechanisms exist in these plants. The complete genome sequence of the cyanobacterial strain *Synechocystis* 6803 showed six different genes, annotated as Na^+/H^+ antiporters (Kaneko et al. 1996), of which at least three were functioning (Inaba et al. 2001). The occurrence of rather large gene families for Na^+/H^+ antiporters clearly point to a group of proteins that fulfill many important functions in osmotic acclimation of cyanobacteria and probably of seaweeds as well. Various studies showed that proton-pumping activity can be directly switched on in salt-treated cyanobacteria due to increased respiratory activity or because of stimulated activities of specific ATPases (Wiangnon et al. 2007, Hagemann 2011). Other Na^+-export systems such as primary active sodium pumps or transporters might exist in seaweeds, but experimental proof is still lacking.

The much higher concentration of intracellular K^+ than in the external medium clearly points to an active uptake of this important cation from the seaweed exterior. In the genome sequences of cyanobacteria, various K^+ transporters and putative K^+ channels have been assigned as potential candidates for performing the uptake of this cation (Hagemann 2011), and more recently it was reported that all cyanobacteria possess the structural genes for a functional ATP-dependent K^+ transport system consisting of a K^+ permease, an ATPase that provides the energy, and a structural stabilisator (Ballal et al. 2007). Most interestingly, this complex K^+ transport system requires but does not transport Na^+ (Matsuda et al. 2004). Such a direct activation by the presence of Na^+ would nicely explain how the K^+ transport activity is rapidly enhanced under salt stress.

In contrast to Na^+ and K^+ transport mechanisms much less is known about Cl^- extrusion/uptake systems. Although Cl^- was involved in the osmotic acclimation of various eulittoral green algae from Antarctica, the concentration remained relatively low even under hypersaline treatments (Karsten et al. 1991b). This is in accordance with the related temperate green algae such as *Ulva prolifera* (as *Enteromorpha prolifera*) (Young et al. 1987). Except *Acrosiphonia arcta*, all other green algal species studied from Antarctica have typically small cells and a large cytoplasmic:vacuolar ratio (Karsten et al. 1991b). They resemble cytoplasm-rich microalgae, which also tend to maintain low Cl^- values in their cytoplasm (Dickson and Kirst 1986). Cl^- like Na^+ has adverse effects on many enzymes (Gimmler et al. 1984). In addition, ribosomes of plants are not functional in the presence of high Cl^- contents (Ritchie 1988).

In the green alga *Acetabularia* spp. a negative membrane potential was measured and interpreted as primarily caused by an electrogenic Cl^- pump (Wendler et al. 1983). Nevertheless, in eukaryotic algae and cyanobacteria Cl^- transport is still badly understood. In contrast, in some bacteria and other eukaryotes such as invertebrates and humans, various genes encoding Cl^- channels or Cl^-/H^+ exchangers have been described (Jentsch 2008). The underlying proteins assemble to dimers, with each monomer containing an ion translocation pathway (Jentsch 2008). From the available data on these organisms it is reasonable to assume similar Cl^- transport systems for seaweeds.

Although K^+, Na^+ and Cl^- represent the major inorganic ions involved in osmotic acclimation, some seaweeds such as *Laminaria digitata* use NO_3^- to satisfy osmotic and nitrogen requirements (Davison and Reed 1985a). However, there are strong seasonal changes in the cytoplasmic composition of major inorganic and organic osmolytes in this kelp. *Laminaria digitata* accumulates high nitrate concentrations in spring. During summer, this anion is completely metabolized, and the gap in the osmotic potential is filled through the biosynthesis and accumulation of the polyol mannitol. This seasonal increase in mannitol concentration compensates for the intracellular decrease in nitrate rather than for changes in external salinity (Davison and Reed 1985a).

In some green seaweeds such as *Codium decorticatum* (Bisson and Gutknecht 1975), *Acrosiphonia arcta* and *Ulva rigida* (Karsten et al. 1991b) SO_4^{2-} plays an important role as an osmolyte. Some brown seaweeds of the genus *Desmarestia* even contain this anion in the form of free sulfuric acid inside the vacuole resulting in a pH of 1–2 (Eppley and Bovell 1958; Anderson and Velimirov 1982).

The energy requirements for ion transport in seaweed species such as *Ulva lactuca* are equivalent to 10–30% of the energy provided by respiration (Ritchie 1988). It seems that all inorganic ion transporters in seaweeds are generally quite fast systems with much lower requirements for metabolic energy compared with the cost for biosynthesis or degradation of organic osmolytes (Kirst 1990). The formation of an intracellular osmotic potential of 1 osmol kg^{-1} requires 1.2 mol ATP when created by KCl uptake only, but 66 mol ATP when based on sorbitol or mannitol biosynthesis.

5.3.2 Organic Osmolytes

The main physiological strategy of all seaweeds studied so far under saline conditions is to keep particularly the Na^+ and Cl^- concentrations in the cytoplasm as low as possible. Since protein and organelle function (e.g., ribosomes, mitochondria), enzyme activity, membrane integrity and structural macromolecules in seaweeds are adversely affected by these ion concentrations (Kirst 1990), it is now generally accepted that the biosynthesis and accumulation of organic osmolytes in the cytoplasm, although energetically costly, permits the generation of low water potentials without incurring metabolic damage (Karsten et al. 1996a; Yancey 2005; Eggert and Karsten 2010).

In many, but not all, cases the organic osmolytes are identical with the main photosynthetic product, and thus there are preferences in different seaweed groups. Polyols such as mannitol are characteristic for most Phaeophyceae, while the Chlorophyta contain typically sucrose, some taxa in addition to proline, glycine-betaine, or dimethylsulphoniumpropionate (DMSP) (Kirst 1990). Although mannitol is present as the sole osmotically significant low-molecular weight organic solute in most brown seaweeds, some species are capable of synthesizing a second polyol (Davison and Reed 1985b). The top-shore Phaeophyceae *Pelvetia canaliculata* contains the heptitol volemitol as an additional intracellular organic solute (Kremer 1976), while the lower shore brown alga *Himanthalia elongata* from the Northern hemisphere as well as various Southern hemisphere Fucales (e.g., *Bifurcariopsis capensis*, *Hormosira banksii*, *Xiphophora chondrophylla*) accumulate the hexitol altritol as isomeric solute in addition to mannitol (Chudek et al. 1984; Wright et al. 1987).

In the Rhodophyta a multitude of low-molecular-weight carbohydrates have been identified in recent years (Eggert and Karsten 2010). The main photosynthetic product in members of most orders of red seaweeds is clearly the heteroside floridoside (α-D-galactopyranosyl-(1-2)-glycerol), while most members of the Ceramiales (Florideophyceae) generally synthesize and accumulate instead of floridoside, the chemically related digeneaside (α-D-mannopyranosyl-(1-2)-glycerate) (Kremer 1978).

Already Lindberg (1955) provided evidence that, in addition to floridoside, members of the Bangiales (Bangiophyceae) contain an isomeric form of floridoside, isofloridoside (α-D-galactopyranosyl-(1-1)-glycerol). Wickberg (1958) later reported isofloridoside in *Porphyra umbilicalis* as a uniform mixture of D- and L-forms. More recently, the chemical structures and configurations of all three heterosides from *Porphyra perforata* were investigated, and the occurrence of floridoside along with both D- and L-isofloridoside was verified (Meng et al. 1987), while the strong involvement of all these compounds in the process of osmotic acclimation was experimentally proven in *P. columbina* (Karsten et al. 1993a). More interesting is the observation of different heteroside patterns in *Porphyra* species from different biogeographic regions in Europe, Africa, North America, Asia, and Australia (Karsten 1999). The composition of the three compounds varied among the species studied. In *P. columbina* from Australia, L-isofloridoside was always quantitatively dominant, while floridoside was the major component in *P. dioica* from the North Sea. D-Isofloridoside was usually present in small concentrations, except in *P. perforata* from the Pacific coast of the USA where it occurred in equal concentrations along with floridoside and L-isofloridoside (Karsten 1999). These results point to species-specific different enzymatic activities of the underlying anabolic pathways, which are, however, not completely understood.

The consistent presence of digeneaside together with a new compound was noted in some members of the genus *Hypoglossum* (Delesseriaceae, Ceramiales), and a chemical survey in members of this taxon resulted in the identification of digalactosylglycerol (2,3-dihydroxypropyl (α-D-galactopyranosyl)-(1→6)-ß-D-galactopyranoside), which was strongly involved in osmotic acclimation (Karsten et al. 2005). Surprisingly, digalactosylglycerol has never been reported for any other seaweed species before, even though it most probably represents the main photosynthetic product in *Hypoglossum barbatum* and *H. heterocystideum* (Karsten et al. 2005).

The disaccharide trehalose was detected in several members of the Ceramiales. While some taxa of this order such as *Aglaothamnion* spp. exhibited only trehalose, others such as *Delesseria sanguinea* showed trehalose together with digeneaside. Although more recent data indicate that only a few Ceramialean taxa are capable of synthesizing trehalose (Karsten et al. 2007), the summarized results in the review of Craigie (1974) point to other Florideophycean species also forming this disaccharide. Therefore, this compound may be more widely distributed among the Rhodophyta than currently thought.

Most interesting is the fact that in some Ceramiales such as in the mangrove-associated genera *Bostrychia* and *Caloglossa* as well as in some early diverging red algal lineages the polyols mannitol, sorbitol, and dulcitol can be found (Karsten and

West 1993; Karsten et al. 1994, 1999, 2003b; Eggert and Karsten 2010), which are otherwise uncommon for red algae.

With the exception of digeneaside that plays no more than a minor role in osmotic acclimation of Rhodophyta (Karsten et al. 2005; Eggert and Karsten 2010), all other low-molecular-weight carbohydrates act as organic osmolytes. Since these organic compounds can be accumulated and tolerated at high intracellular concentrations, and permit the generation of low water potentials without incurring metabolic damage (Yancey 2005), the term "compatible solute" was introduced by Brown and Simpson (1972). In general, the intracellular concentrations of these organic osmolytes are actively adjusted by photosynthesis driven de novo biosynthesis or by remobilization of storage products and are directly proportional to external salinity (Kirst 1990).

Although differing in their chemical structure, compatible solutes in seaweeds have some features in common: they are typically highly soluble, in most cases have no net charges at physiological pH, and are non-inhibitory at high concentrations (Kirst 1990; Karsten et al. 1996a). The interactions of these organic compounds with intracellular macromolecules are not completely understood and several mechanisms have been suggested. Bisson and Kirst (1995) discussed different models to explain the protection of enzyme systems: (1) binding of the solute to the protein, (2) colligative action of the solute, (3) buffering of potentially damaging changes in solution properties, (4) inhibition of conformational changes resulting in formation of inter- or intramolecular disulfide bridges, and (5) preferential exclusion of the solute from the protein surface. These models can be basically summarized into two types: (1) those that hypothesize direct solute–protein interactions and (2) those that postulate that protein stability is mediated by solute-induced changes in water structure (Roberts 2005; Yancey 2005). However, there is little experimental evidence in seaweeds for any of these models.

Desiccation tolerant seaweeds such as supralittoral green algal *Prasiola* or brown algal *Pelvetia* species typically exhibit morphological adaptations such as thick cell walls that protect against rapid water loss and the capability to synthesize and accumulate polyols as "water-keeping" substances (Jacob et al. 1991, 1992).

5.3.3 Biosynthesis of Organic Osmolytes

Kremer and Kirst (1981) showed that exogenously applied inorganic ^{14}C is rapidly taken up by various red algae and assimilated into floridoside, which is thus acting as a major photosynthetic product. The biosynthesis of floridoside is initiated by a condensation reaction of l-glycerol-3-P and UDP-galactose resulting in floridoside-P. This reaction is mediated by a respective heteroside-P synthase (Kremer and Kirst 1981). Floridoside-P is subsequently de-phosphorylated by a specific phosphatase. In this anabolic pathway l-glycerol-3-P serves as precursor, and the condensation reaction takes place at the C-2 position of glycerol. In contrast, the biosynthesis of D- and L-isofloridoside in the Bangiales is unknown.

The biosynthesis of digeneaside in red algae is initiated by a condensation reaction of L-glycerate-P and UDP-mannose resulting in digeneaside-P. This reaction is mediated by digeneaside-P synthase, and followed by a specific digeneaside phosphatase which de-phosphorylates digeneaside-P (Kirst 1990).

All members of the mangrove red algal genus *Caloglossa* synthesize the polyol mannitol under salinity stress (Karsten and West 1993). The biosynthesis of mannitol was experimentally verified for the first time in *Caloglossa leprieurii* (Karsten et al. 1997). This species exhibits four enzymes that control the size of the mannitol pool. Mannitol-1-P dehydrogenase (Mt1PDH; EC 1.1.1.17) reduces fructose-6-P to mannitol-1-P. Mannitol-1-phosphatase (Mt1Pase; EC 3.1.3.22) subsequently dephosphorylates mannitol-1-P and releases mannitol in the anabolic pathway. The catabolic pathway includes the conversion of mannitol to fructose by mannitol dehydrogenase (MtDH; EC 1.1.1.67) and further to fructose-6-P by hexokinase (HK; EC 2.7.1.1.). Both pathways involved in mannitol metabolism are known as the so-called mannitol cycle (Karsten et al. 1997).

A current study on the key enzyme mannitol-1-P dehydrogenase in the brown alga *Ectocarpus siliculosus* took advantage of the recently published genome (Cock et al. 2010; Rousvoal et al. 2011). Applying a biochemical and for the first time a genomic approach, the latter authors documented a salt-induced gene expression and upregulation for this enzyme, i.e., hypersaline conditions stimulated the formation of mannitol. Similarly, Iwamoto et al. (2003) documented the biochemical and kinetic properties of purified mannitol-1-P dehydrogenase from *Caloglossa continua*, and also reported strong enzyme regulation by salinity.

In contrast to the mannitol metabolism, the biosynthesis of sorbitol and dulcitol as well as of trehalose in red seaweeds is unstudied. Nevertheless, a trehalose-6-phosphate synthase gene was recently screened out from a large DNA fragment library constructed from *Porphyra yezoensis* (Dai et al. 2004), indicating the genotypic presence of a trehalose biosynthesis key enzyme. This example strongly supports the usefulness of various recent genomic projects on different seaweed taxa, which will give a deeper look into the molecular mechanisms of biosynthesis and regulation of organic osmolytes.

5.3.4 Antioxidants

Since seaweeds perform oxygenic photosynthesis using water as an electron donor they steadily release molecular oxygen, which can be accumulated and easily chemically converted to potentially damaging reactive oxygen species (ROS). The sources and production sites of ROS are mainly related to photosynthetic activities, such as pseudocyclic photophosphorylation and the Mehler reaction, which stimulate the accumulation of hydrogen peroxide (Asada 1994; see Chap. 6 by Bischof and Rautenberger). Besides these internal processes, formation of ROS might also be induced under hypersaline conditions as reported for *Ulva fasciata* (Sung et al. 2009). These authors undertook a gene expression study and documented a salt-induced upregulation of various antioxidant enzymes such as superoxide dismutase, ascorbate peroxidase, glutathione reductase, and catalase, which efficiently detoxified ROS.

5.3.5 Ultrastructural Changes

In many seaweeds, the separation of the plasmalemma from the cell wall rather than cell volume changes under hypersaline conditions is the most damaging aspect of plasmolysis (Reed 1990). However, in some species such as the red alga *Caloglossa leprieurii*, the elastic cell walls accommodated marked shrinkage of the protoplasm when treated with hypersaline media resulting in a concomitant swelling and hence prevention of plasmolysis (Fig. 5.2, Mostaert and King 1993). These authors suggested that the enormous flexibility of the cell wall thickness may be a protective mechanism in response to fluctuating salinities.

Besides the adverse ionic influences on particular sites of the photosynthetic machinery, the cellular ultrastructure may also be affected by salt stress resulting in reduced photosynthesis and respiration. In *Porphyra umbilicalis* changes in the thylakoid structure of the chloroplasts after salt treatment have been described (Wiencke 1982). Hypersaline conditions typically result in cell shrinkage due to water loss with thylakoids and membranes appressed, and under hyposaline conditions cellular organelles are typically swollen. This disturbance of fine structure may cause a disruption of energy transfer in photosynthetic electron flow (Satoh et al. 1983). In contrast to chloroplasts, mitochondrial cristae ultrastructure is less affected by salinity changes (Kirst 1990), and this well explains the better functioning of respiration compared to photosynthesis under the respective stress.

Another ultrastructural observation is the formation of vacuoles after hypo- or hypersaline stress in seaweeds such as *Porphyra umbilicalis*, which under normal conditions contain only very few of these organelles (Wiencke and Läuchli 1980). The vacuoles formed under hypersaline conditions may serve as compartments to sequester metabolically toxic ions, mainly Na^+ and CI^- (Wiencke et al. 1983). Concomitantly, the fine structure of the tonoplast changes is probably related to the intensity of ion transport across it (Wiencke and Läuchli 1983).

5.3.6 Self Protection

In addition to active processes, which compensate for osmotic stress, *Laminaria* blades form multiple-layered, mat-like canopies at neap tides, protecting the individual thalli against desiccation and salinity changes (Lüning 1990). Macroalgal canopies of *Ulva* sp. in the upper littoral zone in southern Spain form under emersed conditions sheet-like, multiple-layered structures in which the top layer usually bleaches due to strong insolation, desiccation, and other abiotic stresses, thereby providing photoprotection and moisture for subcanopy thalli (Bischof et al. 2002).

5.4 Salinity Ecotypes

Habitats with strong horizontal salinity gradients such as estuaries or the Baltic Sea promote genetic adaptation and eventually speciation. Indeed, the geographic semi-isolation from the Atlantic and the steep horizontal salinity gradient of the Baltic Sea have caused local genetic adaptation in several seaweeds and contributed to the formation of so-called ecotypes. Ecotypes (*sensu* Turesson, 1922) are genetically distinct populations of a species that are locally adapted to particular environmental conditions. The ability of populations to adapt to a novel habitat is a key component of the speciation process. Ecotypes are recognized as physiologically distinct variants of a species. The concept of ecotypes is widely accepted in relation to ecophysiological diversity in seaweeds when considering salinity stress responses. Several Baltic seaweeds were physiologically and morphologically compared with their marine counterparts and a number of salinity ecotypes have been described such as *Ceramium strictum* (Rueness and Kornfeldt 1992), *Delesseria sanguinea* and *Membranoptera alata* (Rietema 1993), and *Fucus vesiculosus* (Nygard and Dring 2008). But data from other regions also clearly point to strong ecotypic differentiation between populations of the same seaweed species such as estuarine and marine isolates of *Pylaiella littoralis* (Bolton 1979), *Polysiphonia lanosa* (Reed 1984), *Bostrychia radicans*, and *B. moritziana* (Karsten et al. 1993b, 1994). Although the kelp genus *Laminaria* is stenohaline (Bartsch et al. 2008), ecotypic differentiation in terms of growth under different salinities has been reported in North Atlantic populations of *Saccharina latissima* originating from Long Island Sound, New York, and Cape Neddick, Maine (Gerard et al. 1987), and might be considered as a mechanism to adapt to locally environmentally unfavorable conditions. However, in most seaweeds the underlying molecular mechanisms of ecotypic differentiation are unstudied.

One exception is *Bostrychia tenuissima*, which is restricted to Southern Australia and New Zealand. Previous studies have revealed two distinct patterns in the presence of osmotically active polyols. Southern Australian populations only have sorbitol whereas northern Australian populations have in addition to sorbitol also dulcitol. These polyol patterns led to speculation on ecotypic differentiation in both population types (Karsten et al. 1995). Using molecular approaches, a 100% congruence was found between polyol patterns and three plastid haplotypes observed among all isolates studied, which experimentally proved for the first time a genetic basis for different ecotypes of the same seaweed species (Zuccarello et al. 1999).

5.5 Outlook

Since the review of Kirst (1990) on salinity tolerance in algae not much scientific progress has been made in seaweeds. In strong contrast, in cyanobacteria many molecular mechanisms involved in osmotic acclimation have been successfully addressed (Hagemann 2011). The main reason for this huge gap in knowledge between both organism groups is related to available genome information. Without genomic data or other modern approaches such as metabolomics or proteomics, it is still difficult to evaluate molecular mechanisms, such as ion transport across membranes, biosynthesis of organic osmolytes, gene expression, and regulation. Therefore, the establishment of more genomes of model seaweeds is urgently needed to get a fundamental understanding of salinity and desiccation stress responses. A first step has been recently taken with the brown alga *Ectocarpus siliculosus* (Cock et al. 2010), so that deeper insight into the molecular biology of osmotic acclimation can be expected in the near future.

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Chapter 6
Seaweed Responses to Environmental Stress: Reactive Oxygen and Antioxidative Strategies

Kai Bischof and Ralf Rautenberger

6.1 Introduction

In an oxygenated environment virtually all metabolic processes involving the transfer of electrons bear the potential hazard of oxygen radical formation. In biological systems the photosynthetic and respiratory electron transport chains (ETCs) located in the thylakoid membranes of chloroplasts and in the inner mitochondrial membrane, respectively, are prominent sites for the evolvement of oxidative stress because of the omnipresence of molecular oxygen (O_2). Reactive oxygen species (ROS) are generally considered as intermediates of O_2 with an unpaired electron; this applies to the superoxide radical ($\bullet O_2^-$), singlet oxygen ($^1O_2$), and the hydroxyl radical ($\bullet OH$). Additionally, due to its high reactivity resulting in major oxidative functions, hydrogen peroxide (H_2O_2) is commonly also included in the group of ROS.

Oxidative stress is considered to be a major component in the cellular stress response of any organism exposed to any kind of environmental stress. As in particular the photosynthetic ETC, and here especially the pseudo-cyclic electron flow (also referred to as “Mehler reaction” or “photoreduction of oxygen”) passing electrons from PSI to molecular oxygen, is one of the most important sources for the formation of oxygen radicals, the ROS evolving pathways in plants and algae have been studied quite intensively (Asada and Takahashi 1987; Polle 1996; Ledford and Niyogi 2005). The Mehler reaction is typically active as a photoprotective

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mechanism under conditions of restricted electron drainage, resultant from e.g., saturated photosynthetic secondary reactions (i.e., Calvin–Benson cycle) and accumulation of reduced NADP ($NADPH + H^+$). These conditions are typically induced under excessive irradiance conditions. Nowadays, it is common knowledge in plant sciences that a sudden exposure to high irradiance of photosynthetically active radiation (PAR: 400–700 nm) may impair or even destruct the photosynthetic apparatus, particularly in low light adapted plants (Andersson et al. 1992; Osmond 1994). Excessive radiation conditions may thus result in an inhibition of photosynthesis, called photoinhibition (Aro et al. 1993; Osmond 1994; Hanelt 1996; Franklin et al. 2003; see Chap. 1 by Hanelt and Figueroa). Furthermore, studies on intertidal seaweeds have shown that besides excessive radiation most other environmental factors leading to physiological stress, like e.g., freezing, desiccation, hypo- and hypersalinity, heavy metals, as well as wounding may accelerate the cellular production of ROS (Benet et al. 1994; Collén and Davison 1999a, b; Burritt et al. 2002; Lu et al. 2006; Pereira et al. 2009; Wu et al. 2009a, b; see also Chap. 5 by Karsten). In general, if accumulation of ROS exceeds the scavenging capacity of enzymatic and nonenzymatic antioxidant systems, remaining non-detoxified ROS may inhibit photosynthesis and become auto-destructive to cells due to the oxidation of lipids, proteins, and nucleic acids. Consequently, the ability to control oxidative stress, i.e., to limit the generation of ROS effectively, is an important feature of organisms inhabiting variable environments. It is, thus, of vital importance to e.g., intertidal macroalgae to suppress or remove stress-induced ROS in order to thrive in their challenging habitat [see Davison and Pearson (1996) for review]. Particularly in the intertidal, macroalgae are subjected to a highly variable environment, which requires permanent adjustments of metabolic rates and protective strategies to keep oxidative stress at minimum, nondestructive levels. Most intertidal macroalgae are exposed to large fluctuation in irradiance levels, i.e., when low tide coincides with high solar radiation conditions around noon (Davison and Pearson 1996). Furthermore, drastic changes in (air and water) temperatures, salinity, desiccation, as well as mechanical forcings represent significant stress factors to intertidal macroalgae with implications to the respective reactive oxygen metabolism (Collén and Davison 1999a; Burritt et al. 2002; Sung et al. 2009).

Besides its major role in stress responses and as mediator of cellular damage, ROS also have been identified forming an important component in signal transduction pathways (Mackerness et al. 2001) and even interspecific interactions. The function in pathogen defence or fouling control via oxidative bursts has been proven by the light-independent release of H_2O_2 triggered by membrane-bound NADPH oxidases (Potin 2008). The present contribution, however, focuses on the stress-mediated induction of ROS, forced by the respective abiotic environment and highlights adaptive and acclimatory traits in macroalgae to cope with oxidative stress in particular with respect to superoxide dismutase (SOD) activity. For extended information on the significance of reactive oxygen to seaweed physiology and biotic interactions, the reader is referred to the recent and very comprehensive reviews by Dring (2005) and Potin (2008).

6.2 Stress-Induced ROS Production and Its Effects on Seaweed Performance

Being photoautotrophic organisms conducting oxygenic photosynthesis, macroalgae display the same major generation sites for oxygen radicals as identified for higher plants. Any malfunction of photosynthesis triggered by an unfavorable environment will finally be reflected by an increase in the level of internally generated ROS. As photosynthetic primary reactions are directly related to the generation of oxygen radicals, hampered dissipation of excessive PAR has been identified as an important inducer of ROS formation in plants (Asada and Takahashi 1987; Asada 1999; Bischof et al. 2002, 2003; see also Chap. 1 by Hanelt and Figueroa). Excessively absorbed light energy may result in an over-excitation of chlorophyll *a* molecules present in the photosynthetic reaction centers, which may then pass into the so-called triplet state. The critical characteristic of this process is that triplet chlorophyll (^{3}Chl) may subsequently promote the formation of $^1O_2$, which is highly reactive with any kind of cellular component (see Ledford and Niyogi 2005). Higher plants as well as algae try to avoid formation of ^{3}Chl by dissipation of excess radiation energy by the xanthophyll cycle, in which energy is dissipated harmlessly as heat by the interconversion of specialized xanthophylls located in the antennae (see Jahns et al. 2009). In addition, ^{3}Chl may be deactivated by carotenoid associated to the photosynthetic reaction centers (β-carotene and lutein).

A second and quantitatively by far the most important source of ROS formation in photosynthesis is the formation of $O_2^{\bullet -}$ in the process of Mehler reaction or photoreduction of oxygen: At a high reduction state of ferredoxin (e.g., under high light conditions, or in case electrons are not drained off at sufficient pace under varying stress conditions), electrons coming from PSI might be transferred to O_2 rather than to ferredoxin, which generates $O_2^{\bullet -}$ (Asada 1999). This ROS may subsequently reduce metal ions like Fe^{3+} and Cu^{2+} univalently. The $O_2^{\bullet -}$, however, is quenched via the enzyme SOD, yielding O_2 and H_2O_2. The latter, highly reactive compound may also either react with the formerly reduced metal ions ("Fenton reaction": Fe^{2+} and Cu^{+}) or with another $O_2^{\bullet -}$ ("Haber–Weiss reaction"). In both cases, the extremely reactive •OH is formed (see Dring 2005). This aggressive compound initiates free radical cascades and may denature proteins, nucleic acids, and peroxidise lipids, potentially resulting in biochemical dysfunctions and structural damages such as membrane leakage. As plants do not have specific protective agents against •OH, the only means of protection is to scavenge both the $O_2^{\bullet -}$ and H_2O_2 as fast as possible and to suppress metal ion reduction (Asada 1999). Moreover, H_2O_2 may also harm multiple biological components, and therefore, it has to be detoxified as well. This is achieved by the enzyme ascorbate peroxidase (APX). In order to minimize destructive effects by H_2O_2 via free diffusion across biological membranes, APX is located closely to SOD in the neighborhood of PSI as well. Its cofactor, ascorbate, is regenerated by the vitamin's two oxidized forms: monodehydroascorbate (MDHA) and dehydroascorbate (DHA). The enzymes glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), and dehydroascorbate reductase (DHAR) as well as glutathione are involved in the regenerating process often called ascorbate–glutathione (AsA–GSH) cycle. In contrast to higher plants, seaweeds are additionally able to detoxify H_2O_2 by excretion out of the cell into their environment (Ross and Van Alstyne 2007). It has been shown for the chlorophyte *Ulva rigida* that H_2O_2 excreted from the thallus can reach concentrations up to 4.0 μM in the surrounding seawater (Collén et al 1995; Collén and Pedersén 1996). Catalase (CAT) is another enzyme that cleaves H_2O_2 to oxygen and water, but it seems that this enzyme exclusively detoxifies H_2O_2 produced by glycolate oxidase in peroxisomes during photorespiration (Gross 1993). Collén and Davison (2001) concluded from their studies on the seaweed *Fucus vesiculosus* that CAT activity is regulated independently of the other components of the reactive oxygen metabolism like SOD and GR and, thus, of light. Because photorespiration is low at low temperatures, an increased CAT activity is unlikely to be detected at suboptimal seawater temperatures. In *Ulva rigidia*, no significant CAT activities have been detected when exposed to several high light environments and only APX increased its activity (Collén et al. 1995). Peroxidase enzymes (PX) need the presence of a reducing substrate e.g., ascorbate and glutathione which are regenerated in the AsA–GSH cycle. Another PX is glutathione peroxidase (GPX), which has been intensively studied in mammalian tissues and higher plants, but much less is still known for this enzyme in seaweeds (Eshdat et al. 1997; Contreras et al. 2009).

Interestingly, the above-mentioned enzymes for oxidative stress management (SOD and CAT) have hardly been reported for kelps (i.e., the representatives of the brown algal order Laminariales). A single DNA sequence likely encoding for SOD was isolated from the gametophyte of *Laminaria digitata* (Crepineau et al. 2000; see Bartsch et al. 2008), but the further analysis of 1985 gene transcripts did not reveal the expression of any of these enzymes in *L. digitata* (Roeder et al. 2005). Instead, it is apparent that the stress-induced expression of bromoperoxidases is involved in oxidative stress management. These enzymes are typically catalyzing the oxidation of halide ions to hypohalous acid, in the required presence of H_2O_2. It was shown that haloperoxidases in *Laminaria* are mainly located near the cuticle in the external cortex region of the thallus (Almeida et al. 2001) and around the mucilaginous channels specifically in *L. hyperborea*. In *Saccharina latissima* and *L. digitata* bromoperoxidases were only found being active in the blade (Jordan et al. 1991; Mehrtens and Laturnus 1997). Oxidative stress in kelps was shown to increase halomethane production (Palmer et al. 2005) and the inhibition of photosynthetic electron transport. Consequently, elevated H_2O_2 production via the Mehler reaction reduced the halogenation process (Goodwin et al. 1997). Haloperoxidase is thus considered as another key enzyme for oxidative stress management in kelps, and in this respect further studies on other ecologically important species of seaweeds are urgently needed (see Bartsch et al. 2008).

Next to ROS-scavenging enzymes there is a suite of a large number of different nonenzymatic intermediate metabolites present which confer antioxidative properties and thus may additionally or alternatively be employed to ROS scavenging in macroalgae, like e.g., ascorbate, glutathione, carotenoids, etc. Today's definition of antioxidants also includes polyphenols, vitamin A and retinoids, vitamin E (α-tocopherol), and various sulfur compounds. Hitherto, various phenolic compounds, carotenoids, as well as mycosporine-like amino acids (MAAs) (Karsten et al. 1998; Aguilera et al. 2002b; Schoenwaelder 2002) have been identified as potential antioxidants from Arctic macroalgae. However, currently little information is available from field studies on the antioxidative potential of Antarctic macroalgae. Interestingly, some MAAs which have received significant research attention due to their UV-screening capacities have also been found to reveal some antioxidative potential (de la Coba et al. 2009), which presumably makes them part of a general stress response in red macroalgae (see also Chap. 20 by Bischof and Steinhoff). Again, there is evidence that the cellular concentration and composition of antioxidative compounds in seaweeds are highly species-specific and dependent on the external environmental forcings (Collén and Davison 1999a, b; Lohrmann et al. 2004).

Although low surrounding temperatures can lead to adverse effects on the metabolic functioning, they also may modulate the impact of high irradiances quite substantially. It has been shown that the combination of high PAR at low water temperature may confer adverse conditions to Antarctic macroalgae (Becker et al. 2010). The reason behind is likely to be a temperature-dependent reduction in photosynthetic secondary reactions (i.e., the Calvin–Benson cycle) resulting in a reduced reoxidation of NADPH, and consequently in an elevated reduction state of ferredoxin (Asada 1999). However, while photosynthetic secondary reactions are strongly temperature controlled, primary reactions are not. Thus, high irradiances of PAR will pump electrons into the photosynthetic ETC and, at the high reduction state of ferredoxin, a considerably higher share of electrons will be fuelled into the Mehler reaction, yielding an increased concentration of $O_2^{\bullet-}$. These environmental conditions are frequently observed in shallow waters of polar and cold-temperate regions (Collén and Davison 1999b, 2001; Becker et al. 2009, 2010). The impact of temperature on the reactive oxygen metabolism was studied by Collén and Davison (2001) in the cold-temperate intertidal brown alga *Fucus vesiculosus*. Here, particularly the increase in the ROS-scavenging activity of SOD has been shown as a characteristic feature, which was related to experimental temperature fluctuations. This, however, might also be highly significant in terms of responses to seasonal changes in the abiotic environment, which are most pronounced in cold-temperate regions.

For completeness, it should be noted that apart from the chloroplasts, other important ROS generation sites in plants are the inner mitochondrial membrane. There, superoxide radicals might be generated, e.g., by the NADPH-dependent electron transport involving the cytochrome P-450. In peroxisomes and glyoxysomes, H_2O_2 formed via enzymatic reactions (by glycolate oxidase and acyl-CoA oxidase) is rapidly degraded by CAT to oxygen and water (see Dring 2005). However, with respect to the quantitative significance toward ROS generation under abiotic environmental stress these processes seem to be of minor importance in plants and seaweeds. The generation of oxidative stress has been largely attributed to the result of a stress-induced impairment/restriction of electron flow, as it may be evidently the case under e.g., excess radiation, temperature stress, and nutrient limitation. The induction of ROS formation by mechanical stress, however, has been a matter of debate and has now been more attributed as an oxidative burst response, similar to the responses upon wounding of the thallus (Collén and Pedersén 1994; Ross et al. 2005; see Dring (2005) and Potin (2008) for review).

There is a multitude of adverse effects that ROS may confer to biological components. One prominent target of ROS is biological membranes, i.e., the lipids, which are differentially sensitive depending on their respective saturation state. ROS-induced peroxidation of membrane lipids results in the formation of aldehydes, e.g., malondialdehyde as readily shown for a variety of marine macroalgae under excessive radiation conditions, both in the PAR and ultraviolet (UV) range (Bischof et al. 2002, 2003, 2006; Dummermuth et al. 2003). Due to their complex structures, proteins are also highly susceptible to the interaction with ROS. A multitude of ROS impacts on proteins have been described, interfering on all levels, the primary, secondary, and tertiary structure of proteins, e.g., by specific interaction with the respective amino acids involved based on their differential substitutes (see Dring 2005). For example, in enzymes ROS may impact on active centers, and in particular ROS-induced impairments of iron–sulfur centers have been described to result in inactivation of enzyme function (see Dring 2005).

An important, visual result of oxidative stress is “photobleaching”: the loss of photosynthetic pigments like chlorophyll due to their photo-oxidation. This phenomenon has been frequently observed in seaweeds exposed to high PAR (Bischof et al. 2002, 2006). In example, loss in pigmentation in response to steep microscale gradients of solar exposure has been studied within green macroalgal mats (Vergara et al. 1998; Bischof et al. 2002). Supported by high nutrient loads, the green macroalga *Ulva rotundata* may form thick mats consisting of multiple thallus layers. Within these assemblages a steep gradient of irradiance persists, which results in different physiological effects. Whereas the pigments in the top layers (canopy) are directly exposed to solar radiation and become visibly photobleached, subcanopy algae suffer from light limitation. Under the high and prolonged radiation conditions, the canopy algae may become completely bleached within 2 days of exposure. The drastic loss in chlorophyll is accompanied by an increase in malondialdehyde levels, which is an indicator for light stress-induced lipid peroxidation (Bischof et al. 2002, 2003). High production of malondialdehyde was also observed in the top layers of mats of another green seaweed, *Chaetomorpha linum*, however, with not as pronounced changes in chlorophyll concentration as in the latter species (Bischof et al. 2006).

6.2.1 Seaweed Exposure to Heavy Metal Stress and Reactive Oxygen Metabolism

Very recent studies have highlighted the particular significance of heavy metal exposure for the induction of oxidative stress in seaweeds. In natural seawater, concentrations of heavy metals are usually very low. Because copper (Cu^{2+}) concentration ranges between 0.05 and 3 g L^{-1} (Contreras et al. 2005, 2009), it is a micronutrient, which is used as cofactors for enzymes (e.g., oxidases, SODs) and ETC components (e.g., plastocyanin). However, due to industrial activities such as copper mining, Cu^{2+} concentrations may rise significantly when highly contaminated wastewaters are drained off into coastal areas. Ecologically, such an impact reduces species richness as well as changes the structures of coastal communities. Consequently, only opportunistic macroalgae, characterized as highly copper tolerant, are able to grow under these extreme conditions. For example, copper-impacted coastal areas with 25 g L^{-1} and higher in northern Chile are inhabited by only two macroalgal species (*Ulva compressa*, *Scytosiphon lomentaria*), although *Lessonia nigrescens* dominates related, but pristine, ecosystems (Contreras et al. 2009).

Macroalgae, independently of their heavy metal-tolerance, are able to accumulate copper in their tissues as a function of its concentration in seawater (Ratkevicius et al. 2003; Andrade et al. 2006). Tissues of *U. compressa* form copper-impacted sites; an approx. 40-fold higher copper content was measured than in conspecifics from pristine habitats (Ratkevicius et al. 2003). These free copper ions (Cu^{+}, Cu^{2+}), which are not bound in protein complexes in the cell, are able to increase ROS production substantially by their involvement in the Haber–Weiss and the Fenton reaction (Pinto et al. 2003). The highly reactive hydroxyl radical (•OH), which is a product of both reactions, changes and inactivates biological macromolecules by oxidation and peroxidation. Therefore, macroalgae exposed to copper excess showed increase in lipid peroxidation, indicating cell membrane damage. If oxidative stress is not sufficiently detoxified by the cellular ROS-scavenging system, it may consequently lead to cell death.

However, the antioxidant defence system is also activated by copper excess. A general response of macroalgae seems to be the stimulation of those enzymes that are involved in scavenging of lipid and fatty acid peroxidation. In copper-tolerant macroalgae (*U. compressa*, *Ulva fasciata*, *S. lomentaria*), activities of APX and peroxiredoxin (PRX) detoxifying H_2O_2 and fatty acid hydroperoxides increased significantly as a result of copper excess. This response is attributable to enhanced gene expression providing new enzymes rather than modulation of already existing enzymes, which represents an efficient acclimation mechanism to cope with copper stress (Contreras-Porcia et al. 2011). In *U. fasciata*, ROS acts as a signal for upregulation of genes encoding for antioxidant defence enzymes (FeSOD, APX, GR) because their transcript levels increased by exogenously applied H_2O_2 concentrations above 0.2 mM (Wu et al. 2009a, b). Moreover, induction of transcription of antioxidant enzyme genes by copper led to an increase in activities of MnSOD, FeSOD, APX, CAT, and GR to cope with copper stress successfully. However, at high copper concentrations (above 20 μM $CuSO_4$), copper might be responsible for a selective inhibition of APX and CAT, which resulted in an insufficient ROS detoxification with enhanced H_2O_2 accumulation and lipid peroxidation (Wu and Lee 2008). However, one must take into account that these mechanisms of copper acclimation are species-specific rather than a general response.

Different efficiencies of buffering oxidative stress-induced by copper excess (20–100 g L^{-1}) might play a crucial role for the absence of the copper-sensitive *L. nigrescens* and the presence of the copper-tolerant *S. lomentaria* in copper-enriched coastal areas in Chile (Contreras et al. 2009). H_2O_2 formed right after copper stress was completely scavenged in both species but much slower in *L. nigrescens* than in *S. lomentaria*. Additionally, lipoperoxide production detected in both species over a 96 h period might be a result from the activation of a lipoxygenase (LOX) that only uses arachidonic acid as substrate. Both species show different responses to copper excess. A stable lipoperoxide production in *S. lomentaria* which was reached early after exposure to copper excess could be ascribed to the constant LOX activity as well as to an efficient ROS scavenging by increased activities of APX and GPX. These enzymatic responses seem to be crucial for macroalgal survival since potentially toxic peroxides are converted into nontoxic compounds. In contrast, continuously increasing accumulation of lipoperoxides in *L. nigrescens* over the entire period might be a consequence of the biphasic boosts in LOX activity. Additionally, inactivation of GPX and APX possibly due to direct inhibition by copper might be a reason for a further accumulation of fatty acid hydroperoxides and H_2O_2 at high copper concentrations. Impaired detoxification may trigger the production of the highly reactive, short-chain aldehydes such as 4-hydroxy-2(E)-nonenal (HNE) which are cytotoxic, genotoxic, and mutagenic due to its electrophilic properties (Guéraud et al. 2010). Dysfunctions of proteins and destruction/changes in the fine structures of mitochondria and chloroplasts in *L. nigrescens* are a consequence of the accumulation of lipoperoxides. Thus, an efficient detoxifying mechanism seems to be crucial for survival of macroalgae in copper-impacted habitats.

6.2.2 A Peculiar Antioxidant System in Kelp

An unusual antioxidant system that is based on the enzymatic oxidation of accumulated iodide (I^-) has been recently described to be present in the sporophytes of the kelp *L. digitata* (Küpper et al. 2008). Two types of vanadium-dependent haloperoxidases (vHPOs) can be found in this life stage to mediate the oxidation of halides (X^-) under consumption of H_2O_2 to hypohalous acids (HXO), which may subsequently react to form iodocarbons such as polyhalomethans (CH_2I_2):

Bromoperoxidases

$$Br^- + H_2O_2 \rightarrow HBrO + OH^- \text{ and}$$
$$I^- + H_2O_2 \rightarrow HIO + OH^-$$

Iodoperoxidase

$$I^- + H_2O_2 \rightarrow HIO + OH^-$$

Although multimeric aggregates of several bromoperoxidases (vBrPOs) oxidize both iodide (I^-) and bromide (Br^-) ions, these enzymes are not involved in the iodide antioxidant system because of their inefficient catalysis toward iodide (see below) as well as their various locations in the cell (Colin et al. 2003). Numerous studies did demonstrate that iodide-oxidizing enzymes, iodoperoxidases (vIPOs), play the central role in the iodine metabolism rather than vBrPOs. These homodimeric enzymes being encoded by a multigenic family are responsible for both iodide uptake and ROS scavenging. They have a strict specificity to iodide because of their special halide binding site topology and the fine-tuning of the vanadate cofactor electronegativity (Colin et al. 2005; Pacios and Gálvez 2010). Iodoperoxidases have a lower affinity to iodide ($\mathrm{Km,I^- = 2.5\ mM}$) and, more important, a higher catalytic turnover rate of iodide ($\mathrm{kcat,I^- = 462\ s^{-1}}$) than vBrPOs ($\mathrm{Km,I^- = 18.1\ mM}$, $\mathrm{kcat,I^- = 38\ s^{-1}}$). Moreover, a seven times higher specific activity toward iodide of the purified iodoperoxidases compared to vBrPOs (cf. 1,200 vs. 180 $\mathrm{U\ mg^{-1}}$) represents a high efficiency of iodide incorporation and the crucial role in iodine metabolism (Colin et al. 2003).

When *L. digitata* is unstressed and submerged during high tide, iodide is taken up from seawater (0.3 μM) probably by facilitated diffusion down its concentration gradient to the apoplast (Küpper et al. 1998). There, the iodoperoxidases mediates the oxidation of iodide. However, this process requires a steady flow of H_2O_2 into the apoplast, which was estimated to as small as approx. 5 μM (Küpper et al. 1998). So far, the source of H_2O_2 is not absolutely clear yet, but it is supposed to be produced by cell wall oxidases or membrane-bound enzymes with an extracellular domain. Intracellular sources of H_2O_2 might also be responsible for the functioning of the iodoperoxidase. However, it lacks detailed studies, which investigate the role of vIPOs under, for example, high light conditions when H_2O_2 is produced by APX or the photorespiratory pathway in response to excessively absorbed light energy.

Depending on the age of the sporophyte and the regions of the thallus, iodide may accumulate between 13,000 and even 150,000-fold relative to natural seawater in the apoplast of *L. digitata* (Küpper et al. 1998). In contrast to these vast pools, iodide contents in related *Ectocarpus* and *Fucus* species are only a fraction of that one found in Laminariales (Saenko et al. 1978; Cock et al. 2010). This substantial difference can be ascribed to the lack of iodoperoxidases in species of these genera. Only bromoperoxidases being characterized by their substrate preference to bromide over iodide fix comparable small amounts of iodide. This is supported by the recent analysis of the genome sequence of *Ectocarpus siliculosus*, which revealed that only one haloperoxidase, a vBrPO, is encoded (Cock et al. 2010).

In the apoplast, iodide is non-covalently associated with biomolecules such as phenolic compounds, polysaccharides, and proteins (Verhaeghe et al. 2008; Küpper et al. 2008). This unique type of accumulation ensures that iodide can be readily and rapidly mobilized for chemical defence and under oxidative stress conditions during high tide (Verhaeghe et al. 2008). It was demonstrated by extracellular addition of elicitors (e.g., oligoguluronates) mimicking pathogen attack and oxidants (e.g., H_2O_2) to *L. digitata* that iodide is released into the seawater within seconds after addition. This response represents a very fast mechanism to acclimate to an external abiotic and biotic stressor. However, because these high iodide concentrations are not directly toxic to both pro- and eukaryotes (Küpper et al. 2008), iodocarbons with high toxicity might also be used to prevent from microbial assault. In fact, iodocarbons such as CH_2I_2 (diiodomethane) and CH_3I (iodomethane) were emitted after oligoguluronate treatment (Palmer et al. 2005). Moreover, oxidative burst in the apoplast is triggered by the recognition of oligoguluronates (Küpper et al. 2001) and bacterial lipopolysaccharides (Küpper et al. 2006). Superoxide anions probably produced by an oxidase with a flavoprotein subunit (i.e., NADPH oxidase) in this process become subsequently converted to H_2O_2 that can diffuse into the seawater. There, H_2O_2 may affect settling of microorganisms on the thallus surface. In the apoplast where organic antioxidants such as ascorbate and glutathione are absent, accumulated iodide is released under oxidative stress conditions to detoxify ROS. Enzymatically, vIPO catalyzes the removal of H_2O_2 by reoxidation of iodide. Furthermore, due to fast, nonenzymatic reactions of iodide with O_3, $^1O_2$, and superoxide anions, these ROS can be scavenged efficiently, which makes iodide the best antioxidant available in the apoplast of *L. digitata* (Küpper et al. 2008). At the end of the oxidative stress period, the iodide remaining in the surrounding seawater is taken up again to the apoplasm where it is re-associated with biomolecules (Küpper et al. 2008).

During low tide events when the thallus is uncovered by water (desiccation stress) and simultaneously exposed to high photon fluxes (high light stress) and O_3 concentrations (ozone stress), iodide may have a significant impact on atmospheric chemistry. Molecular iodine (I_2) is released directly from the surface into the atmosphere above the kelp beds by the abiotic reaction of O_3 with accumulated iodide. Then, I_2 is photolytically (impact of high light) broken down to the iodine radical ($I^\bullet$) on the thallus surface. The $I^\bullet$ reacts with O_3 in the troposphere to IO (iodine oxides) providing a precursor for aerosol particles (>3 nm) that may lead to cloud condensation nuclei formation. Particle formation seems to be a result from O_3-scavenging reactivity of iodide on the thallus surface (Küpper et al. 2008) rather than by the iodine atom-releasing breakdown of iodocarbons as presumed earlier (O'Dowd et al. 2002). So, taken all these impacts together, the iodine metabolism in kelps has not only a great impact on ROS scavenging in the apoplast and the extracellular defence but also on atmospheric chemistry.

6.3 Antioxidative Strategies in Seaweeds on Seasonal and Spatial Scales

For all seaweeds living in highly variable environments, it is essential to apply protective and detoxifying mechanisms to scavenge and to minimize the adverse effects of oxygen radicals, which are resultants from abiotic environmental stress (Collén and Davison 1999a, b; Rijstenbil et al. 2000; Bischof et al. 2003).

As already indicated above, macroalgae apply a multitude of enzymatic and nonenzymatic tools to reduce the impact of ROS on their biological/cellular structures. Studies on Arctic and cold-temperate macroalgae demonstrated the plasticity of the

ROS-scavenging mechanisms in order to protect against cytotoxic reactive oxygen. These mechanisms include the inducible increase in activities of the radical scavenging enzymes SOD, APX, GR as well as the cellular concentration of antioxidants, e.g., glutathione, ascorbate, carotenoids (Aguilera et al. 2002b; Dummermuth et al. 2003).

SOD has often been referred to as "the first line of defence" against ROS. However, in most of the studies conducted on SOD activity in macroalgae so far, it was not discriminated between the different isoforms of SOD, the cytosolic Cu/Zn-SOD or the Fe-SOD located in chloroplasts, neglecting the assumption that it is indeed the combination and interaction of different isoforms of SOD characterizing it as the central protection mechanisms against $O_2^{\bullet -}$-mediated damage (Pinto et al. 2003; see Dring 2005). Variation in total SOD activity has been found among different seaweed species and also with respect to the respective growth site, i.e., abiotic stress exposure along latitudinal or vertical gradients (Aguilera et al. 2002b). In general, *inter*specific differences in SOD activity are mostly related to differences in the respective abiotic environment of the species under investigation, depending on latitudinal differences, but also the shore level, which is typically populated by the respective species. In their survey on general antioxidative properties of polar macroalgae, Aguilera et al. (2002b) reported on an interspecific depth-dependent antioxidative pattern: species from the upper shore are generally characterized by higher SOD activities than those from deeper growth sites as a likely consequence of high light exposure.

Latitudinal differences in SOD activity were found in the closely related green macroalgae *Ulva bulbosa* (now also referred to as *U. hookeriana*) and *Ulva clathrata* from Antarctic and sub-Antarctic regions, respectively (Rautenberger and Bischof 2006). Total SOD activities in *U. bulbosa* were significantly higher (86–89 Units mg^{-1} protein) compared to those in *U. clathrata* (58–63 Units mg^{-1} protein). Apparently, these differences based on the respective geographical dispersal of these species are resultant from differences in water temperature and radiation regimes, modulated by latitude. The Antarctic ecotype of *U. bulbosa* is permanently exposed to lower water temperatures (around 0 °C) than *U. clathrata* isolated from waters in which temperatures never decrease below 5 °C. Exposure to lower water temperatures may permanently cause a higher background level of ROS in *U. bulbosa* which requires a more efficient detoxification system, reflected by the higher SOD activity. Furthermore, *U. bulbosa*'s lower susceptibility to enhanced irradiances of UV-B radiation at 0 °C might be a consequence of a more efficient photoprotection, possibly achieved by higher SOD activities as well.

On a smaller spatial scale, i.e., with respect to growth at different shore levels, the related intertidal rhodophytes *Mastocarpus stellatus* and *Chondrus crispus* (Gigartinales) have been tested for their respective total scavenging activity of SOD, which was found to be clearly related to general stress tolerance (freezing, high light, temperature) and tidal height (Collén and Davison 1999c; Bischof et al. 2000; Lohrmann et al. 2004). Also, different intertidal congener species of the brown alga *Fucus* display differential overall activities of SOD, positively correlated with the respective position of the respective species on the shore (Collén and Davison 1999a, b).

6.3.1 *SOD Activity in the Brown Seaweed* **Desmarestia anceps** *Along a Depth Gradient: A Case Study in Antarctica*

In line with *inter*specific variation of SOD activity along gradients of different spatial scales, also *intra*specific variations have been found, reflecting the specific abiotic conditions in individuals of species growing over pronounced latitudinal and/or vertical ranges.

The variation of SOD activity with depth was studied in an ecologically important brown seaweed from Antarctica (Rautenberger and Bischof, previously unpublished data): The endemic Antarctic phaeophyte *Desmarestia anceps* colonizes water depths between 5 and 30 m in coastal ecosystems (see also Chap. 13 by Wiencke and Amsler). Occurring across such a wide range within the sublittoral zone, this species is subjected to a pronounced vertical gradient of habitat stability. Thus, individuals from highest positions on the shore are regularly exposed to frequent and strong changes in abiotic conditions, such as solar radiation, whereas specimens from deeper waters inhabit a much more stable environment. It was, thus, expected that *D. anceps* has a high potential to respond to environmental changes at the individual growth sites by metabolic adjustments to the respective in situ conditions.

Overall, the species-specific capacity to detoxify ROS with respect to environmental stability, also including the exposure to detrimental UV-B-radiation, is a major factor determining the vertical distribution patterns of seaweeds on the shore (Bischof et al. 1998; Aguilera et al. 2002b; see Chap. 20 by Bischof and Steinhoff). In *D. anceps*, site-specific variation of total SOD activity as a function of water depth was investigated in adult sporophytes. Individuals were collected at 5.5, 9.0, and 13.5 m water depth, near the Antarctic scientific base Jubany (62.23°S, 58.63°W) at King George Island (South Shetland Islands, Antarctic Peninsula) in January 2005. Specimens were cultivated in air-bubbled basins in the laboratory at 15 μmol m^{-2} s^{-1} PAR (16:8 h light/dark) and 2 ± 1°C for 10 days. Changes in SOD activity in response to exposure to enhanced ultraviolet radiation were studied by supplementing the PAR regime with 15.3 W m^{-2} UV-A and 2.2 W m^{-2} UV-B. For exposure, Petri dishes containing the specimens were completely covered by cutoff filters in order to expose experimental individuals to a defined spectral composition: PAR alone (400–700 nm), PAR + UV-A (320–700 nm), and PAR + UV-A + UV-B (280–700 nm). Consequently, the integral UV-B dose over the entire experimental period of 4 h was 31.8 kJ m^{-2} and the three radiation treatments were used to study *D. anceps*' potential to acclimate to enhanced UV-B radiation by SOD adjustment. SOD activities were determined according to a modified xanthine/xanthine oxidase assay of McCord and Fridovich (1969) and Aguilera et al. (2002b) at 25 °C. Initial total SOD activities (PAR alone) were related to the original water depths where the individuals of *D. anceps* have grown before collection (Fig. 6.1a). Individuals obtained from 5.5 m exhibited very high activities of 2,760 ± 2,283 Units mg protein^{-1}. Although SOD activities of 1,389 ± 559 Units mg protein^{-1} determined in individuals from 9.0 m showed a trend to lower values, there was no statistical difference in SOD activity in specimens from both depths. However,

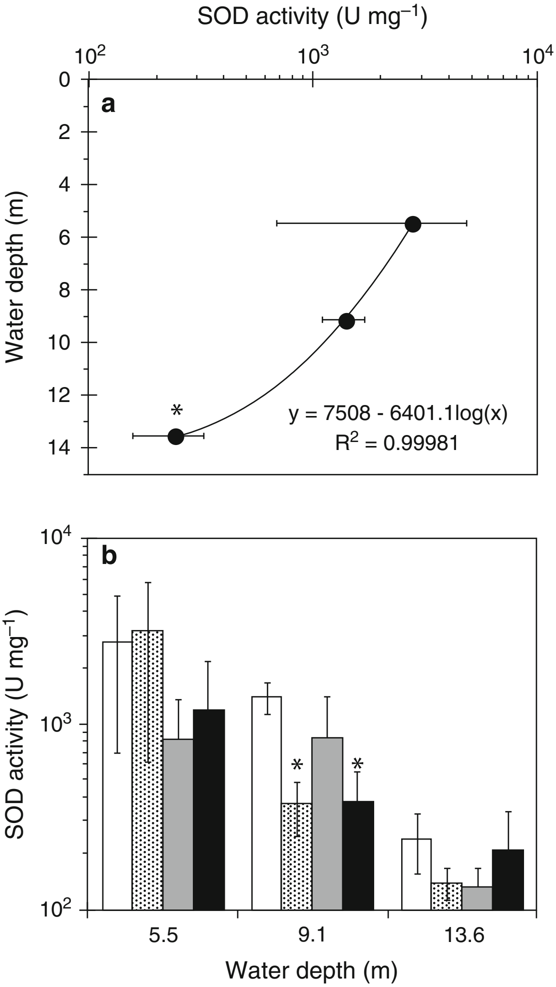

Fig. 6.1 (**a**) Total activities of superoxide dismutase (SOD) in individuals of *Desmarestia anceps* collected from 5.5, 9.0, and 13.5 m water depth before UV exposure. Activities were fitted according to a logarithmical function. (**b**) Changes of SOD activities after 4 h of exposure to PAR alone (control, *dotted columns*), PAR + UV-A (*grey columns*), and PAR + UV-A + UV-B (black columns) in comparison to initial SOD activities before UV exposure (*white columns*). Error bars characterize standard deviations. The *asterisks* represent statistical differences between SOD activities of individuals from different depths (**a**) or light treatments (**b**). Note that the SOD activities are plotted logarithmically

individuals from the deepest position tested (13.5 m) revealed significantly lower SOD activities of 241 ± 184 Units mg protein^{-1}. SOD activities of *D. anceps* from each water depth did not change in the course of the 4 h exposure to either UV-A or UV-B radiation compared to samples under PAR alone (Fig. 6.1b).

Thus, the results presented suggest that *D. anceps*' capacity to detoxify the superoxide radical formed under conditions of environmental stress (here: artificial UV radiation) is strongly related to environmental variability, i.e., according to original growth depth: high SOD activities may protect shallow water individuals of *D. anceps* efficiently against ROS induced by environmental stress. The intra-specific adjustment of SOD activity thus seems to represent a crucial mechanism of acclimation along environmental gradients. However, although UV-B radiation is regarded to be an important factor determining macroalgal vertical distribution

(Bischof et al. 1998; see Chap. 20 by Bischof and Steinhoff), this factor did not seem to play a major role in ROS formation under the experimental conditions tested, since SOD activities did not increase, even not in individuals from the deepest collection site. Also, results obtained do not point to a highly flexible response of SOD adjustment, at least not within the 4 h of experimental exposure. Thus, data obtained rather reflect long-term acclimatory adjustments, potentially allowing the efficient detoxification of light-induced superoxide in individuals from the upper and mid sublittoral (5.5 and 9.0 m), where irradiance conditions may increase and may become harmful to photosynthesis on sunny days, as soon as noon coincides with low tides. In contrast, low SOD activities shown for the deep-water individuals (13.5 m water depth) reflect the larger degree of habitat stability as e.g., the extent of attenuation of solar radiation by the water column above and the in situ radiation climate. However, high SOD activities of *D. anceps* are presumably achieved by increasing the cellular content of the scavenging enzyme rather than by modification to the protein itself. Consequently, higher energetic costs for protein biosynthesis might then be compensated by higher photosynthetic activities as demonstrated in *D. anceps* from the upper sublittoral.

As outlined above, the variation in SOD activity described in individuals of *D. anceps* resulted from site-specific differences in habitat stability and light attenuation along the depth gradient, in the present case approximately 10 m. Other studies, however, explored whether changes in SOD activities are also significant along microscale gradients of light exposure, e.g., within algal canopies where irradiance might be diminished within just a few centimeters. In fact, in dense algal assemblages exposed to high solar irradiance, distinct responses of SOD activities toward variation in light quantity and quality have been observed in green algal mats of *U. rotundata* and *C. linum* (Bischof et al. 2002, 2003, 2006). Results obtained over microscale gradients confirmed the findings on *D. anceps* that overall SOD activity represents well the in situ radiation climate and thus the vertical position of respective specimens, but does not exhibit changes in activity and thus flexible adjustments under experimental conditions. These adjustments seem to require a longer exposure to the respective environmental conditions in order to become significant. Thus, the studies mentioned above did not exhibit changes in SOD activity along diurnal or tidal cycles.

6.3.2 Seasonal Changes in SOD Activity in Seaweeds from an Arctic Fjord

The ecological implications of adjustments of the antioxidant metabolism become apparent when considering pronounced *seasonal* changes in abiotic conditions at the natural growth sites of seaweeds. In particular, polar regions represent a good example for such studies because the abiotic environment of macroalgae changes more drastically throughout the seasons than it does in temperate or tropical regions. The modulation of antioxidant enzyme activities with respect to changing radiation and temperature regimes in the course of the seasons has been observed for a number of macroalgal species from an Arctic fjord system: Kongsfjorden, Svalbard (Aguilera et al. 2002a). It was striking that macroalgae growing subtidally, such as the chlorophyte *Monostroma* sp. and the rhodophyte *Palmaria palmata*, showed patterns of antioxidant enzyme activity modulation, which were corresponding to seasonal changes but also to their respective growth site and, furthermore, life strategy. In *Monostroma* sp. and *P. palmata*, SOD activities closely reflected the particular PAR and UV radiation conditions in Kongsfjorden: SOD activities were low as long as the coastline was still covered by sea ice until the middle of June. Thus, these subtidal organisms were exposed to prolonged conditions of extreme low light. The sea ice breakup may then occur rapidly within very few days and is mainly triggered by changes in the hydrographic conditions of the fjord (Svendsen et al. 2002). Accordingly, seaweeds which were exposed to darkness or very low light conditions during the polar night and under the prolonged sea ice cover may then rapidly be exposed to high irradiances of PAR and UV radiation because of the subsequent very clear water conditions. Therefore, high radiation is able to penetrate deeply into the water column and thus even affects subtidal macroalgae significantly. *Monostroma* sp. responded to the breakup of sea ice with more than a doubling of total SOD activity within very few days and with a continued increase as long as the seawater remained clear. Simultaneously, the detected loss of GR activity might either be a result of increased CAT activities or a consequence of direct radiation damage (Aguilera et al. 2002a). *Palmaria palmata* even quadruplicates SOD activity in summer, but this response was much slower than in *Monostroma sp*. Moreover, this increase was still ongoing throughout the summer season and may thus reflect an acclimation pattern to the season. In contrast, SOD activity in *Monostroma sp.* peaked just before the onset of snowmelt inshore and consequently the runoff of turbid freshwater. These events resulted in an increase of suspended material in the water column, leading to a strong decrease in water transparency and thus decline in in situ light exposure. Consequently, SOD activities might well be reduced again under subsequent turbid water conditions. Overall, this very flexible seasonal response in SOD activity of *Monostroma sp.* is in line with the purely opportunistic life strategy of this ephemeric green alga. In contrast to both species described above, the shallow water red alga *Devaleraea ramentacea* did not exhibit marked variation of SOD activity in the course of the seasons. It rather maintained high SOD activities throughout the year, even under low light conditions under sea ice cover. This is typically characterizing *D. ramentacea* as a shallow water species and is in line with the generally reduced habitat stability, being exposed to more pronounced variation in physicochemical variables in shallow waters.

In summary, high interspecific variation in SOD activity has been demonstrated in a multitude of studies, reflecting species-specific differences with respect to the respective growth site along latitudinal and depth gradients, with respect to site-specific seasonal variation, as well as differences with respect to developmental stages, age, and tissue type under investigation. Oxidative stress is also to be considered as an important component of cellular signal transduction pathways (Mackerness et al. 2001), although there is only scant information obtained from seaweeds in this respect. As a consequence of oxidative stress, most organisms, and seaweeds as well, typically increase the expression of specific cell repair-related proteins. Protoplasts of *L. digitata* sporophytes have been shown to massively upregulate heat-shock proteins HSP-70 and HSP-90, which play a crucial role in the recovery of cells from stress, in the prevention of protein aggregation and in the refolding of denaturated proteins (Roeder et al. 2005).

6.4 Oxidative Bursts: Reactive Oxygen and Interspecific Interaction

The significance of reactive oxygen radicals is by no means restricted to be resultant from abiotic stress resulting in a malfunction of photosynthesis. A fast, light-independent induction of massive ROS formation, which is referred to as an "oxidative burst", has been recognized as a tool involved in interspecific interaction like e.g., pathogen defence in marine macroalgae (see Potin 2008 and Weinberger and Potin 2010 for review). In these complex systems, oxygen radicals ($O_2^{\bullet-}$, H_2O_2, or •OH) are transiently formed by the infected or assaulted alga in response to stimuli originating from either the pathogen and parasite or the host's cell wall. These stimuli are often represented by chemical elicitors, as extensively studied in a few red and brown macroalgal species within the last decade.

Chondrus crispus exhibits oxidative bursts upon challenging with its frequent parasite, the green alga *Acrochaete operculata* (Weinberger et al. 2005a; see Dring 2005 and Weinberger 2007 for review). The mechanisms behind ROS and, more specifically, H_2O_2 production by the host upon infection by a parasite is well understood in the *Chondrus*/*Acrochaete* system (Weinberger et al. 2005a): L-asparagine, which is released from the parasite serves as substrate for L-amino oxidase in the apoplasm of the host. Thus, *C. crispus* is able to perceive microbe-associated molecular patterns (MAMPs) which are also referred to as general or exogenous elicitors. The excreted H_2O_2 will result in the inhibition of the parasite's settlement, but may also be quenched again by the presence of host-specific peroxidases.

Red and brown marine macroalgae are able to perceive pathogen-induced molecular patterns (PIMPs) or endogenous elicitors. These elicitors are degradation products of their own cell wall due to the action of lytic enzymes secreted by attacking organisms (Weinberger 2007). In a study in which 17 red macroalgal species of Gracilariaceae were exposed to agar oligosaccharides it was shown that two different mechanisms of defence-related responses to this chemical elicitor exist in this family: (1) oligoagar-activated oxidative burst and (2) oxidation of agar oligosaccharides. In nature, agar oligosaccharides arise when pathogenic organisms cleave the cell wall matrices of a red macroalga enzymatically. In laboratory studies however, this elicitor is used to add to algal media to study their defence responses.

In contrast, oligocarrageenans, which are chemically similar to oligoagars, did not lead to any defence response in *Gracilaria* sp. *"dura"*[1] (Weinberger et al. 1999).

In *Gracilaria* (*Gracilaria* "*sensu stricto*") and the closely related *Hydropuntia* species (Gurgel and Fredericq 2004), agar oligosaccharides induce a fast and transient oxidative burst in which relatively high amounts of H_2O_2 (>100 nmol g^{-1} min^{-1}) are released into the medium after the first challenge. It is assumed that agar oligosaccharides are presumably perceived by cell membrane-bound, specific receptors which may trigger a subsequent signal transduction pathway. In fact, the lack of oxidative burst due to the use of the protein kinase inhibitor staurosporine demonstrates that phosphorylation of signal molecules and/or proteins seems to be crucial to relay the "signal of an attack" toward a H_2O_2 producing agent. A NADPH oxidase located in the plasma membrane appears to be activated by the signal transduction pathway. Inhibitor studies with DPI (diphenylene iodonium), which is a specific inhibitor of NADH- and NADPH-dependent enzymes (Weinberger et al. 2005b), showed that H_2O_2 was not released in species of these both genera. These findings suggest that ROS production for pathogen defence by an activation of a NADPH oxidase requires phosphorylation events in a signal transduction pathway which is triggered by oligoagar-specific receptors.

An alternative mechanism leading to strong H_2O_2 release in response to agar oligosaccharides has been shown to be present in species related to *Gracilaria chilensis* (*G. chilensis* clade) and those of the genus *Gracilariopsis* (Weinberger et al. 2010). In these species, fast H_2O_2 production (<100 nmol g^{-1} min^{-1}) results from direct oxidation of agar oligosaccharides by an agar oligosaccharide oxidase. Inhibitor studies have proven that neither NADPH oxidases nor kinase-mediated phosphorylation events are involved in H_2O_2 release. Moreover, oxidation products of agar oligosaccharides are able to activate expression of genes related to agar oligosaccharide oxidase within the first 24 h after the challenge (Weinberger et al. 2010). In contrast to the members of the *Gracilaria* "*sensu lato*" major clade (*Gracilaria* "*sensu stricto*" and *Hydropuntia*) which show a refractory state of oxidative burst after first challenge, H_2O_2 is repeatedly released without any delay after a previous challenge in species of the "*G. chilensis* clade" and the genus *Gracilariopsis*.

A comparative study of agar oligosaccharide responses within the family of the Gracilariaceae revealed that the activation of a NADPH oxidase may be a relatively "newly" acquired feature because it is only present in the *Gracilaria* "*sensu lato*" major clade (Weinberger et al. 2010). It was speculated by the authors of the study that the activation of a NADPH oxidase can be coincident either with the acquisition of agar oligosaccharide-specific receptors or the signaling pathway that interlinks the receptors with the oxidase (Weinberger et al. 2010). In contrast, direct oxidation of agar oligosaccharides by agar oligosaccharide oxidase seems to be widely distributed in Gracilariaceae because of its activity in the whole

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[1] *Gracilaria conferta* from Israel being used in the study of Weinberger et al. (1999) was recently identified as *G.* sp. "*dura*" and can be classified as a *Hydropuntia* species. However, species belonging to the *G. "sensu lato"* major cluster show the same response as *G.* sp. "*dura*" from Israel (Weinberger et al. 2010).

family. Thus, two mechanisms of H_2O_2 release seem to be coexist in the *Gracilaria* "*sensu lato*" major clade. This pattern reveals that defence response by direct oxidation of agar oligosaccharides is more ancient than oxidative burst triggered by oligoagar (Weinberger et al. 2010).

ROS formation due to perception of PIMPs also occurs in brown macroalgae. In Laminariales, oxidative burst is triggered by recognition of specific degradation products of alginates, being the major polysaccharides in their cell walls. The addition of oligoguluronates, which are homopolymeric blocks of poly-α-1,4-L-guluronic acid, to *L. digitata* induces a transient and strong release of H_2O_2 into the medium within a few minutes. Similar to the *Gracilaria* "*sensu lato*" major clade, the oxidative burst is a result from signal transduction chains triggered by the recognition of the elicitor. The activation of phospholipases and kinases as well as ion fluxes across the plasma membrane is apparently involved in the signaling pathways (Küpper et al. 2001). Moreover, perception of bacterial lipopolysaccharides (i.e., MAMPs) may also induce early events of oxidative burst and fatty acid oxidation (Küpper et al. 2006).

An analysis of the pattern of gene expression in response to oligoguluronate elicitation showed that 50 genes were highly regulated within the first 24 h in *L. digitata* (Cosse et al. 2009). The number of differentially expressed genes which were upregulated was maximal (38 genes) after 6 h and decreased continuously after 12 h (21 genes) and 24 h (12 genes) after challenge. However, six of these differentially expressed genes remained upregulated over the first 24 h. By the use of various inhibitors affecting signal transduction and ROS formation, the expression pattern of ten genes was affected differently. Three trends of changes in transcript levels observed led to the conclusion that three different signal transduction pathways might be involved in oligoguluronate-induced oxidative burst and set the stage for subsequent gene regulation (Cosse et al. 2009). A coexistence of multiple pathways leading to H_2O_2 release due to PIMP perception was shown in the *Gracilaria* "*sensu lato*" major clade as well (Weinberger et al. 2010). One signal transduction pathway appears to be dependent on early phosphorylation events by kinases and has a great impact on expression of *vIPO1* (vanadium-dependent iodoperoxidase 1), *trx* (thioredoxin like 5), and *hsp70* (heat-shock protein 70) genes. A second signaling pathway seems to be fully controlled by the oxidative burst: H_2O_2 production regulates transcript levels of *vBPO3* (vanadium-dependent bromoperoxidase 3) and *g6pd* (glucose-6-phosphate dehydrogenase). The third signal transduction chain apparently depends on both ROS production (oxidative burst) and the activation of putative MAP kinases or other downstream kinases. This pathway led to an upregulation of the *vIPO3* gene whereas the *vBPO1* gene was concurrently downregulated. Based on this finding, Cosse et al. (2009) hypothesized that ROS produced by oxidative burst might also be an internal signal to induced expression of genes with defence-related function. The rapid induction of the *vIPO3* gene encoding a novel vanadium-dependent iodoperoxidase upon oligoguluronate elicitation suggests that the iodine metabolism might be specifically activated on the molecular level during early defence response (Cosse et al. 2009). This is in line with the fast and massive iodide release into the medium after elicitation (Küpper et al. 2008). The simultaneous repression of the *vBPO1 gene* coding for a vanadium-dependent bromoperoxidase indicates a tightly coordinated regulation of these two distinct haloperoxidase gene families (Cosse et al. 2009). This antagonistic response on transcription level might lead to the conclusion that oligoguluronate-induced oxidative burst switches the iodine metabolism on to achieve a more efficient and effective pathogen defence (Cosse et al. 2009).

Stress- and defence-related signals might be responsible for communication between marine macroalgae, e.g., to transmit warning messages to their neighboring conspecifics, as recently demonstrated for *L. digitata* (Thomas et al. 2011). It was shown that elicited sporophytes have a great impact on defence responses to oligoguluronate in un-elicited neighboring conspecifics. It seems that elicited sporophytes release signaling agents (of unknown nature so far) into the surrounding water which are integrated by their neighboring conspecifics. As a consequence of the perception of the putative waterborne signal, *L. digitata*'s capacity to detoxify ROS has potentiated: the pattern of oxidative burst and emission of volatile organic compounds (VOCs) changed as well as genes regulated in response to oligoguluronate become faster induced. This effect resembles the *priming* in terrestrial plants where species that had been in contact with signals borne off infested neighbors show earlier and stronger effects in defence response (Thomas et al. 2011). The less intense oxidative burst in primed sporophytes represented by a significantly earlier decrease in H_2O_2 release after oligoguluronate elicitation may be attributed to a faster triggering of ROS detoxification processes. Lower emission of VOCs might also reflect an enhanced ROS detoxification mechanism. Moreover, the higher and faster elicitation-dependent upregulation of genes involved in ROS management (*prx*, peroxiredoxin, and *msr*, methionine sulfoxide reductase) also represents a more efficient antioxidative response early after elicitation. These responses prepare the primed sporophyte to a better response to subsequent challenges without directly triggering defence responses (Thomas et al. 2011).

In this way, the generation and scavenging of ROS does also play a central role in biotic interactions, which certainly needs to be explored in much more detail.

6.5 Summary

Overall, the formation and effective detoxification of ROS represents a crucial feature in seaweed responses to the abiotic and biotic environment, and it still requires more intense research activities. Hitherto, the mechanisms of ROS-mediated signal transduction pathways in seaweeds are just basically studied. It should also be emphasized that based on the multitude of chemically mediated biotic interactions of seaweeds with their environment, the significance of ROS for grazing and pathogen defences is a challenging but extremely exciting field of future research. With respect to the importance of the oxygen radical metabolism to stress physiology of seaweeds, a general link between ROS formation and habitat stability of the respective growth site is well established. The formation of ROS as resultant from photosynthetic malfunctions, and thus rising from stress generated by extreme radiation salinity and temperature (e.g., freezing) regimes, is apparent, but still the interaction of environmental factors with respect to potential synergistic or antagonistic effects as well as features of cross adaptation needs to be addressed in the future. Moreover, in particular those abiotic factors, which are not directly related to photosynthetic performance, such as mechanical stress, need to be studied with respect to their significance to ROS generation. Considering the generation of ROS as some kind of general stress response of seaweeds under environmental constrains, the need for easy-to-apply as well as for sensitive biochemical assays in order to characterize oxidative stress burdens under in situ conditions becomes apparent. In this respect, interdisciplinary projects between seaweed ecologists and biochemists are particularly promising and should be considered as an essential approach for upcoming studies.

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Part II
Biotic Interactions

Chapter 7
Competition, a Major Factor Structuring Seaweed Communities

Matthew S. Edwards and Sean D. Connell

7.1 Competition Theory

Competition for shared resources has long been viewed as an important structuring agent in natural communities (Gause 1934; Strong 1980). Generally defined as the simultaneous use of limited resources by two or more organisms, competition can negatively impact population growth rates and influence community-level processes such as predation and/or how species respond to disturbances (Roughgarden 1979). This can occur between individuals of the same species or among individuals of different species. Early mathematical models such as those posed by Lotka (1925) and Volterra (1926) and later demonstrated by Gause (1934) suggest that when competition between two species is asymmetrical, one species will eventually drive the other to local extinction in their "struggle for existence." However, these models do not include the effects of other factors (e.g., predation, herbivory, environmental heterogeneity, or extreme environmental conditions) which often mediate the strength and outcome of competitive interactions (reviewed in Olson and Lubchenco 1990). In fact, even though two species rely on a shared resource, they may not compete if that resource is not limited or if the effects of other factors such as grazing or disturbances are substantially greater. However, when the shared resource is limited and competition for it is strong relative to other factors, the outcome of competition may vary as a function of both inter- and intraspecific interactions (Creese and Underwood 1982), especially as they relate to each species' own carrying capacity. Here, one species may drive

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the other to local extinction if the strength of their competitive abilities is asymmetrical, but they exhibit similar carrying capacities. Conversely, if the carrying capacities of the two species are substantially different, the species with the larger carrying capacity can drive the other species to local extinction even if their competitive abilities are equal.

While numerous examples of competition among individuals and/or species exist, debate over the general importance of competition as a structuring agent in natural communities remains. On the one side, Weins (1977) argues that competition among many species is actually rare in nature and that its importance as an agent of natural selection is therefore minimal. On the other hand, Diamond (1978) supports the view of Darwin (1859), who suggested that competition between closely related species is a deterministic factor in natural selection. In fact, Darwin wrote “As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between species of distant genera.” In discussing competition among macroalgae specifically, Miller (1967) notes that competition can occur via direct interactions in which one organism and/or species prevents the other from access to a limited resource (interference competition) or via indirect interactions where the species exploit a shared resource but do not directly interact with each other (exploitative competition). However, given that different algal traits such as rapid and/or indeterminate growth, large thallus size, and resistance to unfavorable environmental conditions can be associated with different competitive interactions, it may be difficult to identify if certain interactions are due to interference, exploitation, or a combination of the two (Olson and Lubchenco 1990). This problem can be exacerbated considering that different ecologists will often use different methodologies in their studies of competition and thus the results of their studies may vary simply due to the experimental approached used (e.g., Underwood and Fairweather 1986), and that experiments aimed at identifying the responses to competition may actually reflect only indirect evidence that it has actually occurred (e.g., Connell 1980). Consequently, demonstrating that competition is important to structuring natural communities requires carefully planned combinations of field observations to identify the patterns coupled with directed manipulative experiments to determine the processes behind them. These methods often involve removing one or more (e.g., the competitive dominant) species(s) and monitoring responses in the other species under consideration. In fact, a large number of studies have used these methods in studies of competition within macroalgal communities and have largely demonstrated the importance of both interspecific and intraspecific interactions as structuring agents. In this chapter, we review some of the main developments associated with these concepts and provide examples from case studies that demonstrate their importance. We focus our discussion on competition among benthic macroalgae, although it should be noted that among bloom-forming microalgae, both exploitative (i.e., for shared limited resources) and interference (i.e., via allelopathy) competition can be important in structuring planktonic communities, especially when the blooms are fully developed (e.g., Solé et al. 2005).

7.2 Competition Among Marine Macroalgae

7.2.1 Overview

The distribution of plants is regulated by both physical and biological factors, though the relative importance of these factors is notoriously variable through time and space, and is particularly dependent on the scale at which they are examined (Dayton and Tegner 1984; Edwards 2004). While plant populations may persist within a given ecosystem due to predation on herbivores as postulated by Hairston et al. (1960), in the absence of herbivory, plants would increase in number and ultimately compete among themselves for light, space, and nutrients. In fact, competition has been predicted to be the most important factor regulating the distribution and abundance of plant species in the absence of environmental stressors (Grime 1974, 1977, 1979). It is considered crucial in setting the latitudinal range limits (e.g., Edwards and Hernández-Carmona 2005; see also Chap. 3 by Eggert and Chap. 18 by Bartsch et al.) and tidal distributions (e.g., Hawkings and Hartnoll 1985) of some macroalgae, and regulating patterns of their succession following disturbances in others (e.g., Sousa 1979). However, the mere presence of a competitor may not be sufficient to cause strong competitive effects. Variation in morphology may have variable effects on the availability of and/or access to resources. For example, the exclusion of erect species from the understory within Australian *Ecklonia radiata* kelp forests depends on the morphology of the algae. Shorter and more flexible forms exclude erect taxa by shading and whiplashing the substratum (Connell 2003a; Irving and Connell 2006), whereas longer and more rigid forms do not exclude erect taxa from the understory which is strongly affected by shade (Kennelly 1987a). These differences have profound effects on the understory communities across Australia as 5,000 km of coastline across the Leeuwin Current (west and south coast) are largely structured by the short-flexible forms whereas the east coast (East Australian Current) understory is structured by the long-rigid forms (Connell and Irving 2009). These mechanisms match closely with variation in understory communities across temperate Australia (Irving et al. 2004). Furthermore, interactions among macroalgal holdfasts may result in strong interspecific competition, as seen in some intertidal red algae in Chile, but little-to-no intraspecific competition, as the holdfasts of the same species tend to coalesce (Santelices et al. 2003). What this means for their populations, however, is uncertain. One thing that is clear is that marine macroalgae are susceptible to competition as space, light, and nutrients are often in short supply in coastal ecosystems (reviewed in Carpenter 1990).

7.2.2 Competition for Light

Light is the primary resource requirement for algal growth, reproduction, and survival. Both the quantity (irradiance) and spectral quality (wavelength) are important in determining the distribution of many algal species, especially along depth gradients in the ocean (Kitching 1941; Saffo 1987). For example, Novaczek (1984) observed that the lower depth limit of *Eckonia radiata* off the coast of New Zealand was set by minimum light requirements of ca 40 mol photons m^{-2} d^{-1}. Conversely, Graham (1996) and Fejtek et al. (2011) found that the shallow limits of *Macrocystis pyrifera* and *Pelagophycus porra* (respectively) were set, at least in part, by high irradiance (PAR) effects on their microscopic gametophytes. Further, high UV-B irradiance appears to be especially important in reducing spore survival and consequently inhibiting algal recruitment in shallow water (e.g., Wiencke et al. 2000; Roleda et al. 2005; see also Chap. 1 by Hanelt and Figueroa and Chap. 20 by Bischof and Steinhoff). With regard to spectral quality, Lüning (1981) examined the effects of blue light on sexual reproduction in gametophytes of *Saccharina latissima* near Helgoland (North Sea) and observed that egg release by the gametophytes was reduced by 50% when they were held under only 1.4 μmol photons m^{-2} s^{-1} of blue light ($\lambda = 449$ nm) for 45 min. However, blue light may also have positive effects, such as enhancing nitrate (e.g., Aparicio et al. 1976) and carbon (e.g., Schmid and Dring 1996) uptake and storage as seen in some green and brown algae, respectively. While irradiance and spectral quality may be important in controlling recruitment, growth, survival, and reproduction in many algae, photoperiod may be as important in controlling the timing of their growth and reproduction. For example, Lüning (1986, 1990, 1994) and Lüning and Kadel (1993) observed that new frond formation in several brown algae is regulated by changes in photoperiod, resulting in circannual rhythms and synchronized seasonal growth. Further, Edwards (1998) observed that recruitment in the brown alga *Desmarestia ligulata* in central California, USA, was closely tied to increase in day length during the early spring, but this was limited to areas where the dominant kelp canopies had been removed either experimentally or by winter storms. In summary, light quantity and quality appear important to macroalgal physiology and thus factors that reduce access to light may be integral in establishing spatial and temporal patterns in their distribution and abundance, especially in the ocean where irradiance rapidly diminishes with increasing depth.

In addition to natural attenuation of light in the ocean (e.g., Kirk 1992), light is absorbed and/or scattered by the macroalgae themselves, placing them in both direct and indirect competition with each other. As a result, many species of macroalgae have developed functional morphology forms that allow them to more effectively capture light for photosynthesis in their respective habitats (Vadas and Steneck 1988). These morphologies range from single cells to multicellular parenchymatous thalli with complex tissue differentiation. Within this later group, many species have evolved morphologies that elevate their photosynthetic blades above their competitors. For example, Kitching (1941) observed that on the shores of Carsaig Island, Scotland, the dominant macroalga *Laminaria digitata* possesses erect nonflexible stipes that hold its blades above the substrate in order to more effectively capture light when occurring in the subtidal where light can be limiting, but flexible stipes that allow its blades to lay prostrate in the water when occurring in the intertidal where light was otherwise abundant but desiccation may be an issue. Similarly, many subtidal kelps produce canopies that are either buoyed at the surface by gas-filled pneumatocysts or are supported above the substrate by thick woody stipes (e.g., Abbott and Hollenberg 1976). These canopies place their photosynthetic blades above those of their competitors and enabling them to more effectively capture light before it reaches their competitors (Horn 1971; Hay 1986). This structure results in a rich mosaic of benthic light regimes below the canopies (Gerard 1984) to which macroalgae can "photoadapt" by altering the amount and/or arrangement of their photosynthetic pigments (Ramus 1981; Rosenberg and Ramus 1982). Combined with other factors such as substrate topography, hydrodynamic forces, and grazing, this can result in benthic algal communities being highly variable at a number of spatial scales (Dayton et al. 1984, 1992, 1999; Foster and VanBlaricom 2001; Edwards 2004).

Much in the way competitive dominance by canopy-forming plants plays a structuring role in terrestrial forest communities (e.g., Brokaw and Scheiner 1989; Connell 1989; Spies and Franklin 1989; Hubbell et al. 1999), shading from kelp canopies can be the determining factor in regulating benthic macroalgal populations (Reed and Foster 1984; Kennelly 1989; Edwards 1998; Connell 2003b). For example, it is well understood that in the terrestrial forests, the removal of only a few canopy dominants can prevent the competitive exclusion of many understory species and thereby promote greater diversity (Whitmore 1989; Brokaw and Scheiner 1989). These understory species can be grouped into three general categories based on how they respond to canopy shading. This "ecological response group" approach has been widely used by terrestrial plant ecologists to classify individual species according to how they respond to changes in their light environment and has been very useful in studies on canopy shading (e.g., Collins et al. 1985; Whitmore 1989; Kursar and Coley 1999). The logic behind the response-group approach is straightforward; canopy removal should elicit positive responses in recruitment and/or growth for species that require high irradiances, negative responses for species that require low irradiances, and little-to-no responses for species adapted to a variety of irradiances (Brokaw and Scheiner 1989; Spies and Franklin 1989; Whitmore 1989; Kursar and Coley 1999). Those species, then, that remain rare under dense canopies but rapidly recruit into canopy gaps or following widespread canopy removal have typically been referred to as "light-adapted," "gap-requiring," or "shade-intolerant" and are often considered to represent fugitive species, while those species that occur under forest canopies but do not markedly respond to canopy loss have typically been referred to as "light-flexible" or "shade-tolerant" species and are often considered to represent climax species (Whitmore 1989; Hay 1994; Clark et al. 2004). Whereas light-flexible species are generally numerically more abundant than light-adapted species both under canopies and in canopy gaps, their ability to withstand low light environments may result in a decreased ability to rapidly respond to sudden increases in light (Canham 1989). As a consequence, light-adapted species, through greater recruitment and growth, typically dominate areas following canopy loss.

In temperate marine communities, where shading by thick canopies of kelps and rockweeds (Orders Laminariales and Fucales, respectively) can regulate understory algal abundance in shallow (<30 m) water (Pearse and Hines 1979; Foster 1982;

Reed and Foster 1984; Kennelly 1987a; Harrold et al. 1988; Dayton et al. 1992), the removal of the dominant canopies typically results in increased bottom light and a corresponding increase in the abundance of opportunistic species (Dayton et al. 1984, 1992; Reed and Foster 1984; Kennelly 1987b; Cecchi and Cinelli 1992; Graham 1996; Edwards 1998). In fact, North et al. (1986) conclude that light is the primary factor regulating species abundances within coastal forests, a claim that has been experimentally tested in numerous studies via experimental canopy removal. For example, Ambrose and Nelson (1982) observed that removal of the invasive *Sargassum muticum* at Santa Catalina Island, USA, resulted in reduced recruitment of the giant kelp *Macrocystis pyrifera* by reducing benthic irradiance. Likewise, Reed and Foster (1984) found that removal of the *Macrocystis pyrifera* surface canopy and the subsurface *Pterygophora californica* canopy in a central California, USA, kelp forest resulted in increased recruitment of understory algae, as well as the kelps themselves. Similarly, Clark et al. (2004) replicated Reed and Foster's canopy clearings at three areas in the same central California kelp forest and followed changes to the understory algae for a period of 2 years. Their clearing design (Fig. 7.1) allowed for the simultaneous testing of the individual and combined effects of shading from both surface and subsurface canopies on understory algal assemblages, and from an opportunistic alga, *Desmarestia ligulata*, that recruited into the clearings in very high abundances. Their results indicated that while understory algae did respond to the canopy clearings, the low abundances of individual species and the small magnitude of each species' response compared to their natural temporal and spatial variability made detecting canopy effects difficult. However, when understory species were grouped together in ecological response groups, they were able to detect otherwise cryptic increases in some (i.e., light-adapted) species as much as 1 year earlier than when each species was examined individually. The exception to this was the opportunistic brown alga *Desmarestia ligulata* which showed dramatic rapid increases within the canopy clearings. Edwards (1998) examined this further and found that while *Desmarestia ligulata* remained in low abundances under existing canopies, it recruited in high abundance in the spring and ultimately reached high bottom cover in areas where the canopies were removed (Fig. 7.2). Similar patterns have been observed for *Desmarestia ligulata* in Point Loma, CA, following canopy removal by winter storms (Dayton et al. 1984) and in three central California kelp forests characterized by different hydrodynamic conditions and canopy covers (Foster 1982). Dayton et al.'s work further described that disturbance to the dominant kelp canopies resulted in variation in the benthic light regimes and a corresponding mosaic of understory algal patches. Some of these patches were able to persist for extended periods of time and competitively exclude or delay recovery of the otherwise dominant kelps. The effects of this canopy shading, however, are not limited to interspecific interactions but also impact individuals of their own species via intraspecific interactions. For instance, shading from the dominant *Macrocystis pyrifera* canopies also inhibits recruitment and growth of their own juvenile sporophytes (Anderson and North 1969; Reed and Foster 1984; Dean et al. 1989). Similar negative effects of intraspecific competition were reported by Neushul and

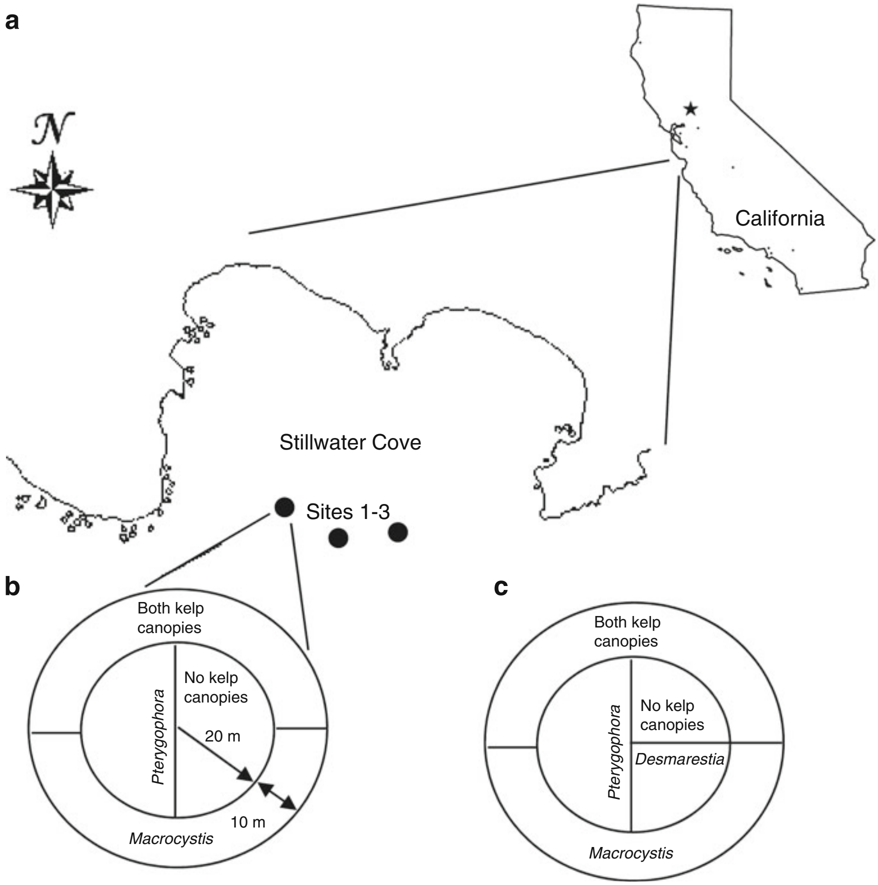

Fig. 7.1 Diagram of kelp canopy clearing experiment used by Clark et al. (2004) showing (**a**) location of the three replicate sites in Stillwater Cove, CA, USA. (**b**) Blocked canopy clearing design showing the 20 m radius inner circles and 10 m radius outer tori from which kelp canopies were removed either individually or in combination. Treatments include "No canopies" = both *Macrocystis* and *Pterygophora* removed, "*Pterygophora* canopy" = *Macrocystis* removed and *Pterygophora* left unmanipulated, "*Macrocystis* canopy" = *Pterygophora* removed and *Macrocystis* left unmanipilated, and "Both canopies" = both kelp species left unmanipulated (also considered as control treatment). (**c**) Canopy clearings showing the placement of the *Desmarestia* removal treatment following dense *Desmarestia* recruitment. Diagram reproduced from Clark et al. (2004)

Harger (1985) and Reed (1987). Consequently, as the dominant kelps begin to recover following a disturbance, they often recruit in much higher densities than can be sustained when they are adults and thus undergo strong intraspecific competition (i.e., density dependence) that results in self-thinning of the population (Fig. 7.3). However, large variability exists in the interpretation of how important density dependence is to algal populations, in part due to differences in the experimental methodologies used to examine it (Flores-Moya et al. 1996; Scrosati 2005).

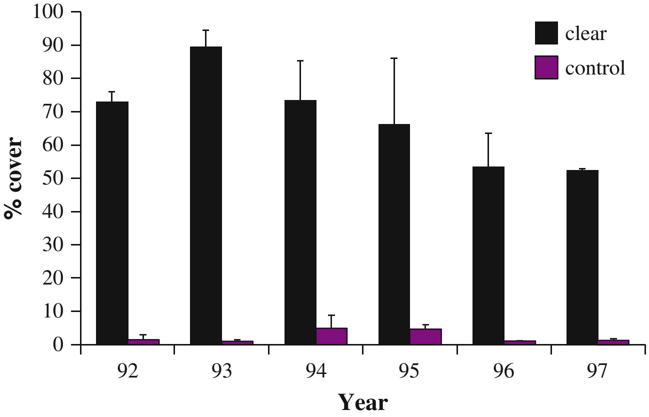

Fig. 7.2 Effects of kelp canopy removal on recruitment (% cover) of *Desmarestia ligulata* sporophytes (means + 1standard error). *Black bars* represent recruitment into areas where kelp canopies had been cleared, and *white bars* represent recruitment into areas where the kelp canopies were unmanipulated (controls) from 1992 to 1997. Reproduced from Edwards (1998)

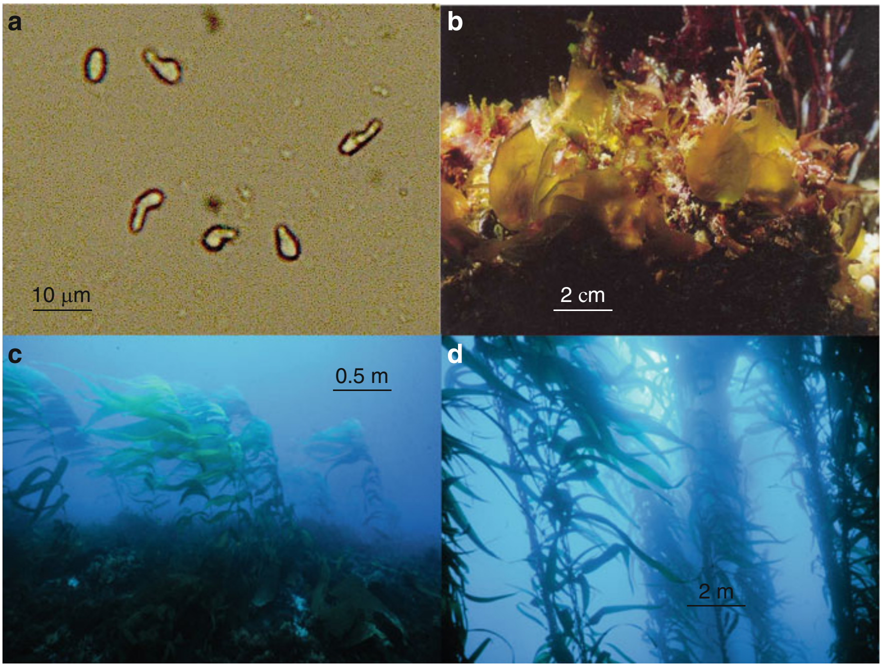

Fig. 7.3 Photographs of giant kelp (*Macrocystis pyrifera*) showing relative densities of different ages as the population self-thins. **a** = young sporophytes (photo taken on a microscope slide), (**b**) recruits, (**c**) juveniles, (**d**) adults. Note the differences in scales showing that younger smaller stages are much more densely packed

Regardless, it is clear that self-thinning is important to many seaweed populations, though this may be more important for unitary species such as *Macrocystis pyrifera* than for clonal species such as *Mastocarpus papillatus* where self-thinning during the growing season is not expected even under high density (Flores-Moya et al. 1996; Scrosati 2006).

While studies along the west coast of North America have shown dramatic responses by the turf-forming algae to kelp canopy clearings, results from other areas of the world are more variable. For example, clearings to the surface and subsurface kelp canopies within *Nereocystis leutkeana* forests in coastal Alaska resulted in complete overgrowth by subsurface kelps within 1 year, while similar clearings within the *Eualaria fistulosa* forest throughout the Aleutian Archipelago resulted in little to no macroalgal recruitment over 1-year period (B. Konar et al. unpublished data). While the reason for this is unclear, we believe it is primarily due to variation in identities and life histories of the species involved (i.e., whether they are annual or perennial), oceanographic conditions (i.e., temperature, nutrient, and wave conditions), grazing pressure, and idiosyncrasies associated with the experiments themselves (i.e., when the clearings were done, how large and thorough they were). However, even with this variability, certain similarities exist among geographic areas. For example, throughout much of Australia, the conditions created by subtidal kelp canopies include reductions in irradiance, sedimentation, and the abundance of turf-forming algae (Kennelly 1987a). Consequently, the kelp canopies maintain encrusting coralline algae from overgrowth by turf-forming algae through shade (Kennelly 1987a; Connell 2003b) and possibly through reduced accumulation of sediments (Melville and Connell 2001). Thus, the clearance of kelp canopies generally leads to the overgrowth of encrusting algae by turf-forming algae, which then trap sediments (Kennelly and Underwood 1993; Connell 2005). Conversely, recovery of the kelp canopies invariably leads to the reverse effect (e.g., Kennelly 1987b), demonstrating that the co-occurrence of canopy and encrusting coralline algae is not just a spatial and temporal coincidence, but rather one driven by the state of the dominant canopy-forming species. Given the strength of association across regions and different taxa in Australia, there appears to be considerable predictive capacity in understanding how the understory macroalgae benefit from the physical light environment created by the canopies (e.g., Bertness and Leonard 1997). These patterns are consistent with the relative abundance of encrusting and turf-forming algae, where the former are relatively abundant in locations of low light and sedimentation (Steneck 1986, 1997), while the latter monopolize locations of high light and high sedimentation (Airoldi 1998).

7.2.3 Competition for Space

On rocky surfaces, access to adequate space is crucial for the attachment and survival of organisms (e.g., Connell 1961). Except for a few examples of free-living algal (e.g., some species in genera *Ulva* (formerly *Enteromorpha*) and

Sargassum, and several species of coralline algae called rhodoliths), most marine macroalgae are attached to rocky reef, other algae, invertebrates, or sediments. This results in their interacting for attachment sites in two dimensions rather than three and thus greatly increases the chances that they will compete for access to the substrate. This will also occur between algae and sessile invertebrates such as is commonly observed on degraded coral reefs where algae are considered competitively dominant to coral larvae and new recruits, but competitively subordinate to coral adults (reviewed in McCook et al. 2001; see also Chap. 16 by Mejia et al. and Chap. 18 by Bartsch et al.). As a consequence, algal proliferation often occurs in areas where coral adults have died, which in turn prevents coral recruitment and slows community recovery (e.g., Kuffner et al. 2006). However, while algal–invertebrate competition is common, we do not address it further here but rather focus our attention to competition between and within algal species.

Although algae may compete strongly for attachment space on the substrate, when examined closely, the actual area of attachment to the substrate is often very small compared to the overall size of the algal thallus. For example, on coral reefs, the actual attachment site of the dominant algae can be as small as 10–100 μm with lots of bare space present between the holdfasts (Hackney et al. 1989). Further, Dayton (1975) found that less than 20% of rocky reef in a subtidal temperate kelp forest was occupied by the kelp holdfasts even though the kelp canopies covered the majority of the reef. Consequently, competition among macroalgae for space, per se, may not be a limiting factor in recruitment in many locations (reviewed in Carpenter 1990). However, given that the thalli of many algae tend to lie prostrate on the substrate or physically abrade the substrate as they move in the waves (Velimirov and Griffiths 1979; Witman 1987; Kennelly 1989), they can prevent settlement and/or growth of other algae on the substrate via interference (abrasion) and exploitative (shading) competition (Duggins and Dethier 1985). Removal of the dominant species, then, generally results in an increase in other macroalgae as observed for intertidal *Hedophyllum sessile* communities in the San Juan Islands, off the coast of Washington State, USA (Duggins and Dethier 1985). Further, some of the strongest competitive interactions in the southern hemisphere tend to be created by large canopy-forming algae (e.g., intertidal *Durvillaea antarctica*; subtidal *Ecklonia radiata*). These individuals exclude many understory species via their fronds which shade or whiplash the substratum (Kennelly 1987b). However, these effects may vary geographically at a number of spatial scales (Connell and Irving 2009) and among different benthic species (Kennelly 1989). Likewise, in the Aleutian Archipelago, physical abrasion from the brown alga *Desmarestia viridis* is an important factor keeping other algae from establishing patches on the tops of pinnacles (Konar and Estes 2003). Physical abrasion by kelp fronds can also prevent recruitment of sessile invertebrates (Connell 2003a) which otherwise monopolize space under lower light and sedimentation such as observed on South Australian coasts (Irving and Connell 2006) or of motile invertebrates that would otherwise graze on the algae (Konar and Estes 2003). Hence, body size often serves as the best measure of the potential for algae and other types of sessile species to exert strong community-wide effects.

Exceptions to the notion that macroalgae do not compete strongly for space have been observed in turf-forming species that can occupy nearly 100% of the substrate in some places and thereby prevent settlement of other algae (e.g., Hruby and Norton 1979), and in areas dominated by encrusting algae which can compete intensely for space (Steneck and Paine 1986). On many temperate coasts, encrusting coralline algae can also occupy up to 80% of hard substrate, dominating space beneath macroalgal canopies (Irving et al. 2004). With the creation of available space (e.g., through storm damage), however, turfs rapidly colonize the space and overgrow the coralline crusts (Russell and Connell 2005; Worm et al. 1999). The morphology of these filamentous turfs allows them to then trap sediment (Airoldi 1998; Gorgula and Connell 2004) and subsequently inhibit the recruitment of canopy-forming species in localities from a diversity of locations around the world (Devinny, 1978; Gorman and Connell 2009). In addition, recruitment of the larger macroalgae can occur on the thalli of the turf algae, though the added hydrodynamic drag on the turf holdfast can result in increased removal rates from waves and thus low survival (Edwards unpublished data). In an example of competition among three species of intertidal crustose and turf algae, Padilla (2003) observed coralline turf algae were better competitors than the upright forms for space, as they were more susceptible to grazing and desiccation. In contrast, two upright forms were inferior competitors for space but were more resistant to grazing and desiccation. Thus, the coralline algae coexisted on the rocky shore, though in different microhabitats. Furthermore, in many temperate systems, if the dominant kelp canopies are excluded from a reef, turf algae may increase in abundance over time and ultimately become the dominant space occupiers, especially in areas where the canopies have been removed (e.g., Edwards 1998; Connell 2003b).

Competition for space itself can be strongly mediated by both physical (disturbance) and biological (competition) factors. For example, Kastendiek (1982) observed three species of algae at Santa Catalina Island, CA, USA, competing strongly with each other but that the nature of this competition differed greatly between species pairs, each of which was influenced by physical disturbances differently. Specifically, the kelp *Eisenia arborea* forms canopies that excludes (or reduces its abundance) the brown alga *Halidrys dioica*, thereby allowing the turf alga *Pterocladia capillacea* to dominate the substrate under the canopy. However, if the *Eisenia arborea* canopy is removed, *Halidrys dioica* recruits in high abundances and dominates the substrate, thus excluding *Pterocladia capillacea* from the area. This switch between competition for light and competition for space appears to be driven by disturbance to the dominant *Eisenia arborea* canopy. Similarly, competition for space may be strongly dependent on species identity and whether the interaction is interspecific or intraspecific. For example, Santelices et al. (2003) observed that in the intertidal region of Chile, when the holdfasts of the intertidal red algae *Mazzaella laminarioides* and *Nothogenia fastigiata* come into contact, one outcompetes the other resulting in its death. However, when the holdfasts of either species come into contact with a member of their own species, the holdfasts coalesce and both individuals survive, suggesting that the populations might be chimeric. Finally, competition for space may be integral in regulating patterns of zonation in the intertidal. Much in the way that Connell (1961) concluded that the upper and lower limits of species distributions in the intertidal may be set by competition and/or predation, Hawkings and Hartnoll (1985) concluded that bands of both dense and sparse macroalgal populations across intertidal shores of the United Kingdom were set by competitive interactions. Specifically, when fronds of the brown algae *Fucus* and *Laminaria* were removed, all other algal species occurring immediately below them were able to colonize further up in the intertidal zone. Similarly, competition may also set the lower limit of those species, as they were also able to colonize the lower parts of the shore following the removal of their competitors.

7.2.4 Competition for Nutrients

Algae require adequate carbon, nitrogen, and phosphorus for growth and survival (see also Chap. 4 by Gordillo), and competition among seaweeds for them has been observed in numerous studies. While the majority of studies on the effects of nutrient limitation have been done for freshwater phytoplankton communities, and have generally reported strong competition for nutrients, their conclusions vary depending on the specific species involved and complex synergies associated with multiple resources (e.g., nitrogen, phosphorus, and silica) that fluctuate independently with one another (e.g., Titman 1976). Unlike freshwater ecosystems, nitrogen (namely nitrate NO_3^-) is the primary limiting nutrient in the ocean, though phosphorus may occasionally be in limited supply. The primary source of nitrogen input into most coastal ecosystems is upwelling of cold nutrient-rich water from below the thermocline, though terrestrial inputs from runoff may also be important in some locations (Gorman et al. 2009). Algae take up the nitrogen directly from the water column via mass transport and thus uptake rates are strongly influenced by thallus morphology ("functional form," surface/volume ratios), tissue and seawater nitrogen content (concentration gradients), and hydrodynamic flow which in turn regulate boundary layer formation around the algal thallus (Hurd et al. 1997). Consequently, during periods of low nutrients and low hydrodynamic flow, algae can compete intensely for nutrients. For example, Dayton and Tegner (1984) report that along southern California, USA, the dominant current flow is caused by longshore currents (see also Winant and Bratovich 1981). While internal waves may be important in cross-shore delivery of nutrients, the longshore currents are the primary source of nutrient delivery into the kelp forest. However, drag imposed on the moving water by the kelp thalli can reduce current speeds within the kelp forest by as much as 33% resulting in reduced nutrient delivery to the inner parts of the forest. Further, the nutrients are taken up by those kelps near the periphery of the forest resulting in further nutrient depletion within the forest. In fact, Jackson and Winant (1983) concluded that nutrient uptake within the Point Loma, CA, USA, kelp forests can be 23% per hour, resulting in the water being nutrient depleted by the time it reaches the interior of the kelp forest, though this may be partially ameliorated by cross-shore delivery of nutrients via internal waves. Consequently, while the individuals near the edge of the forests may be healthy, individuals in the interior can become nutrient stressed and appear less healthy during periods of low nutrient availability, though this varies considerably with forest size (Bernstein and Jung 1979; Dayton et al. 1984). This nutrient limitation may also be important to reproduction in many species. For example, Reed (1990) concluded that both interspecific and intraspecific competition between the microscopic gametophytes of *Macrocystis pyrifera* and *Pterygophora californica* was intense when they settled at high densities but not when they settled at low densities. He attributed this to competition for nutrients even though the culture media was changed regularly. In contrast, Vadas (1972) found no evidence of competition among the gametophytes of *Nereocystis luetkeana*, though this may have been because his overall densities were substantially lower than those used by Reed. Further, Carney and Edwards (2010) observed that delaying development as 1–2 celled gametophytes for 1–3 months can ameliorate the negative effects of intraspecific competition among kelp gametophytes, though she did not test how this impacts eventual sporophyte recruitment.

7.3 Competition in Complex Environments

7.3.1 Synergistic Effects of Different Factors

While it is true that limitation of one or more resources can be important to the recruitment, survival, and reproduction in many macroalgae, synergistic effects among numerous environmental factors may result in substantial variability in how species respond to these limitations. For example, Fujita (1985a, b) reports that when nutrients are plentiful, the green algae *Ulva* spp. (formerly *Enteromorpha*) are able to outcompete the red algae *Gracilaria tikvahiae* for space in the intertidal due to its greater uptake and growth rates. However, *Gracilaria tikvahiae* possesses greater nutrient storage capabilities and therefore outcompetes *Ulva* during periods when nutrients are limited. Likewise, on the New England, USA coast, where the brown alga *Fucus vesiculosus* is the dominant competitor for space over *Ulva* spp. in the absence of grazers, *Ulva* spp. is the competitive dominant species when grazers are present. This occurs because the grazers remove the fast growing young stages of *Ulva* spp., thus allowing the slower growing grazer-resistant *Fucus* to grow. Along the Pacific coast of Baja California, MEX, the giant kelp *Macrocystis pyrifera* forms a surface canopy above the stipitate kelp *Eisenia arborea* and thus outcompetes *Eisenia arborea* for light. However, *Eisenia arborea* is more resistant to low nutrient conditions such as those observed during El Niño Southern Oscillation (ENSO) events (Hernández-Carmona et al. 2001) and thus is able to persist during periods when *Macrocystis pyrifera* dies. Following the ENSO, *Eisenia arborea* is able to form dense subsurface canopies that exclude *Macrocystis pyrifera* recruitment and thus prevent recovery of its populations for several years (Edwards and Hernández-Carmona 2005). Likewise, Dayton et al. (1984) observed similar patterns between *Macrocystis pyrifera* the subsurface kelps *Pterygophora californica* and *Laminaria farlowii* following the 1982–1984 ENSO in a southern California kelp forest. Here, the subsurface kelps were more resistant to the large ocean waves associated with this disturbance and thus exhibited greater survival. Much as with *Eisenia arborea* in Baja California, these kelps were able to delay *Macrocystis pyrifera* recruitment, resulting in longer term changes to the understory algal patch dynamics within the kelp forest. Similar changes to competitive hierarchies have been observed in other areas of the world in response to environmental factors. For example, although *Ecklonia radiata* is generally competitively dominant to turf algae along the South Australia coast, nutrient discharge to the normally oligotrophic waters causes turfs to dominate the space and inhibit recruitment of *Ecklonia radiata* (Gorman and Connell 2009), resulting in a competitive outcome that can persist for several decades (Connell et al. 2008). Finally, Duggins and Dethier (1985) note that while the intertidal kelp *Hedophyllum sessile* outcompetes other algae for space in the intertidal areas of the San Juan Islands, its competitive abilities are regulated by grazing from the chiton *Kathrina tunicata* and by wave exposure, both of which act to remove *Hedophyllum sessile* and create bare space for other algae to recruit. Taken together, it is clear that the competitive abilities of at least some macroalgae can be a trade-off with features that are adapted to the environment. For example, while the giant kelp *Macrocystis pyrifera* develops large canopies above its neighbors and thus outcompetes them for light, its large size and high growth rate make it more susceptible to disturbance from large waves and low nutrients than many of its neighbors (Dayton and Tegner 1984). In their review on competition in seaweeds, Olson and Lubchenco (1990) write, “Because the traits of seaweeds have evolved in a context of multiple selection pressures, the consequences of traits will vary with environmental conditions.” Consequently, a comprehensive investigation of competition in heterogeneous environments requires studying how competition operates under different combinations of environmental conditions.

7.3.2 The Importance of Competition in Maintaining Marine Forests

Marine forests form diverse biological habitats and largely persist by facilitating their own recruitment through the competitive exclusion of opportunistic turf-forming algae (Dayton et al. 1984; Reed and Foster 1984; Connell 2005; Irving and Connell 2006). When kelp canopies are lost, however, turfs rapidly colonize space and inhibit the recruitment of juvenile kelp and reformation of kelp forests (Kennelly 1987a; Gorman and Connell 2009). Under conditions of elevated nutrients, these naturally ephemeral turfs persist in fragmented forests (Airoldi et al. 2008; Gorman et al. 2009) to cause intergenerational decline and collapse of the kelp community (Connell et al. 2008). The competitive dominance of kelps over turfs is a key interaction that enables kelp forests to regenerate and persist, but this dominance may be reversed under conditions that favor the persistence of turfs (Gorman and Connell 2009). As a consequence, it is clear that variation in algal assemblages within and among kelp forests can be attributed partly to differences in the primary canopy-disturbing agents, ocean waves, and temperature (Foster 1975; Cowen et al. 1982; Foster 1982; Dayton et al. 1984, 1992; Seymour et al. 1989; Breda and Foster 1985; Harrold et al. 1988; Graham 1997). This, however, can be highly variable especially on a seasonal scale. For instance, along parts of the west coast of North America, large ocean waves associated with winter storms remove large quantities of kelp canopies, typically resulting in maximum kelp canopies in summer and minimum canopies in winter (Kimura and Foster 1984; Reed and Foster 1984; Dayton et al. 1992). Consequently, competitive interactions between the canopy-forming and understory species can vary temporally, further increasing the overall variation in kelp forest community composition (Pearse and Hines 1979; Gerard 1984; Kennelly 1987a, b; Harrold et al. 1988; Dayton et al. 1999). For example, Edwards and Hernández-Carmona (2005) found that along the coast of Baja California Sur, MEX, the dominant *Macrocystis pyrifera* canopies typically reduce the abundance of the understory *Eisenia arborea* canopies. However, all the *Macrocystis pyrifera* canopies were lost during the 1997–1998 ENSO, resulting in a dramatic increase in *Eisenia arborea* canopies that were able to prevent *Macrocystis pyrifera* recovery at its southern range limit for up to 20 years.

7.3.3 Competition in the Face of Climate Change

The role of global environmental change in driving change to macroalgal communities in marine ecosystems has received heightened attention (e.g., Wernberg et al. 2010, 2011). While range contractions and extensions have been forecast as a function of changing climate (e.g., temperature), the effects on competitive interactions among species are less clear. Unlike kelps, many turf-forming species are ephemeral and require increased resource availability to enable their physiology and life history to be competitively superior to perennial species (Airoldi et al. 2008). Coastal waters that facilitate the expansion of turf-forming algae (e.g., enhanced CO_2, temperature, and nutrients; Gorgula and Connell 2004; Connell and Russell 2010) tend to maintain their dominance of space at the expense of canopy-forming algae (e.g., Gorman and Connell 2009). Much of the global research effort into forecasting the effects of climate change focuses on the direct effects, thereby overlooking indirect effects (e.g., competitive effects). As the name implies, "indirect" effects are not as simple to identify as "direct" effects and can often yield "unexpected results" (Wootton 1994). They are unanticipated because the impact of one species on another (i.e., competitors) requires knowledge of a third species or mediating component is poorly understood. Research into ocean acidification (see Chap. 19 by Roleda and Hurd) is a good case in point. Marine waters absorb approximately 30% of the anthropogenic-derived CO_2 from the earth's atmosphere and the resulting ocean acidification (Feely et al. 2004; Orr et al. 2005) and direct negative effects on calcifying algae. The difficulty is that for noncalcifying algae, elevated inorganic carbon has positive effects on some species and not others, and that these nonuniform effects among alternate species (review by Gao and McKinley 1994) have relatively unexplored consequences to competitive hierarchies, particularly if growth is limited by sources of inorganic carbon.

If competitive interactions are reduced by the increasingly novel conditions brought by human activities, then the persistence of entire biological communities is increasingly likely to be disrupted. Such phase shifts are not uncommon, but anticipating them has been problematic because many involve indirect effects for which the impact of one species (e.g., turfs) on another (e.g., kelp) requires knowledge of a third element that is inadequately understood (e.g., synergies among pollutants). The strength of competition (e.g., dominance of kelp over turfs) is important to understand because it identifies the conditions in which turfs expand. The mere presence of foundation species may not always maintain their competitive strength over turfs. As canopies are thinned, reduced in size, or fragmented, their positive effects are reduced and the associated environmental conditions become more similar to those experienced outside the canopy (Jackson and Winant 1983; Bruno and Bertness 2001). Under these conditions, turfs expand to dominate space and inhibit the recruitment of kelp (Gorman and Connell 2009; Connell and Russell 2010), leading to phase shifts over multiple generations (Connell et al. 2008). Therefore, the maintenance of intact populations of foundation species seems critical to the strength of interaction (i.e., continued dominance over kelp inhibitors) and ensuing maintenance of community structure and function (Bruno and Bertness 2001). The competitive balance between species is often shifted by the abiotic environment which alters the relative abilities of algae to recruit to and retain space. Hence climate change seems set to bring change to competitive processes as we currently understand them.

7.4 Concluding Remarks

In conclusion, competition within and among marine macroalgae is a deterministic influence in establishing patterns of biogeography, regulating growth and reproduction, and in maintaining populations at or below their carrying capacities. It is important to setting species range limits, governing how populations will respond to disturbances, and in structuring coastal ecosystems. However, the direction, strength, and importance of these competitive interactions vary considerably with species identity, the location where these interactions take place, and with changes to the physical and biological environment. Many species have evolved morphologies that enable them to better access the resources, and thus outcompete their neighbors, but these morphologies also may make them more susceptible to environmental stresses, thereby temporarily altering competitive hierarchies and ameliorating the effects of limited resources. Even so, numerous studies have demonstrated that competition can be the most important factor in regulating marine macroalgal population and community dynamics. However, while our understanding of these interactions has grown considerably since Lotka (1925), Volterra (1926), and Gause (1934) wrote their seminal works, information on how these interactions will work in the future remains lacking. Perhaps the most important next step is to assess how these competitive interactions will change under environmental variability, such as predicted with climate change. Understanding this may better inform us of how macroalgal communities will likely be structured in the future.

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Chapter 8
Grazers on Benthic Seaweeds

Katrin Iken

8.1 Common Classification Systems of Grazers

Seaweed grazers can be classified in several ways, most commonly by their feeding mode, their size, or their diet specificity, with continua rather than distinct groups within each of these classifications (Table 8.1). These classifications are not only of practical use for researchers but also have many ecological implications.

First, grazers can be distinguished by functional feeding mode, such as grazing, browsing, rasping, biting, tearing, etc. Grazer mouthparts can be specifically adapted to feeding on seaweeds, and even on particular algal functional groups with different morphological thallus characteristics (thickness, branching, calcification; Littler and Littler 1980). For example, gastropod grazing has been distinguished based on specific radula types (Steneck and Watling 1982), herbivorous fishes can develop specialized mouthparts such as the “beak” in parrot fish, and the Aristotle’s lantern of sea urchins is particularly suitable for grazing on tough kelps. The functional group approach is intriguing to ecologists because it may allow detection of generalizable and predictable patterns in ecosystem functioning rather than focusing on small differences among individual species. This approach, however, may also overemphasize the functional redundancy in a system by obscuring small but ecologically important differences in food selection or assimilation within a particular functional group of grazers. For example, herbivorous coral reef fishes classified within the same functional group displayed strong species-specific food selectivity among algal species, suggesting a low degree of functional redundancy within this feeding group and that species-specific herbivore effects can be missed when looking at functional groups alone (Mantyka and Bellwood 2007).

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Table 8.1 Common classifications of seaweed grazers

Grazer taxon	Feeding mode	Size group	Diet specificity	Typical habitat	Selected examples
Amphipods	Biting Tearing	Mesograzers	Specialists–generalists	Tropical rocky shores/ coral reefs Temperate rocky shores Polar rocky shores	*Pseudoamphithoides* feeds selectively on and builds domiciles from the chemically defended brown alga *Dictyota* (Hay et al. 1990a) *Amphitoe* grazing is driven by food choice and habitat quality of host algae (Duffy and Hay 1991), and can control brown algal biomass and competitive dominance in temperate Atlantic reefs (Duffy and Hay 2000) *Aora* is a generalist feeder on taxonomically and morphologically diverse macroalgae in New Zealand (Taylor and Brown 2006) Amphipods occur in high abundance on Antarctic macroalgae (Huang et al. 2007) and *Gondogeneia* selectively feeds on the red alga *Palmaria* (Amsler et al. 2009; Aumack et al. 2010)
Isopods	Biting Tearing	Mesograzers	Specialists	Intertidal/shallow subtidal temperate fucoid communities	*Idotea* influences biomass and distribution of *Fucus* in the Baltic Sea (Engkvist et al. 2000) and of *Ascophyllum* in the North Atlantic (Viejo and Åberg 2003) *Idotea* controls epiphyte growth on *Fucus* induced by high nutrient loads (Worm et al. 2000; Orav-Kotta and Kotta 2004)
Polychaetes	Biting Tearing	Mesograzers	Generalists	Temperate rocky shores	Herbivorous polychaetes, mostly *Platynereis*, preferentially feed on filamentous and branched algae in the Mediterranean (Antoniadou and Chintiroglou 2006)
Prosobranch gastropods	Rasping Browsing	Mostly mesograzers	Generalists	Temperate rocky intertidal Temperate kelp beds Polar rocky shores	Selective grazing of the periwinkle *Littorina* in rocky tidepools controls abundance of the dominant space competitor *Ulva* (Lubchenco 1978)

					Lacuna grazing at high densities can affect kelp populations and survival (Chenelot and Konar 2007) The abalone *Haliotis* preferentially consumes kelp (mostly drift) in New Zealand (Cornwall et al. 2009) *Laevilacunaria* is a generalist grazer on Antarctic seaweeds, but also depends on epiphytic microalgae (Iken 1999)
Opisthobranch gastropods (Ascoglossa, Anaspidea)	Biting Rasping	Mostly mesograzers	Specialists	Tropical coral reefs	The ascoglossan *Costasiella* selectively feeds on the chemically defended green alga *Avrainvillea* (Hay et al. 1990b) The anaspidean *Aplysia* performs best when feeding on members of the red alga *Portieria* with moderate chemical defense levels (Ginsburg and Paul 2001)
Crabs	Biting Browsing	Macrograzers	Generalists	Tropical rocky shores	*Grapsus* preferentially feeds on filamentous algae; it supplements its diet with animal items when seasonally forced to feed on low nutritional encrusting algae (Kennish 1996)
Sea urchins	Biting Tearing	Macrograzers	Specialists–generalists	Temperate kelp beds Tropical coral reefs	*Strongylocentrotus* grazing causes phase shifts from kelp beds to urchin barrens in the absence of top predators in the Aleutian Islands (Estes and Duggins 1995) *Diadema* grazing removes macroalgae from coral reefs, thus facilitating space for coral growth and recruitment (Carpenter and Edmunds 2006)
Fishes (e.g., Scaridae Pomacentridae Acanthuridae	Biting Tearing Browsing	Macrograzers	Specialists–generalists Specialists–generalists Specialists–generalists	Tropical coral reefs Temperate kelp beds Polar rocky shores	Damselfishes defend territories on coral reefs to "garden" algae on which they feed, thus influencing reef algal and overall communities (Jones et al. 2006)

(continued)

Table 8.1 (continued)

Grazer taxon	Feeding mode	Size group	Diet specificity	Typical habitat	Selected examples
Siganidae Blenniidae) (e.g., Blenniidae Girellidae Kyphosidae Stichaeidae Scorpididae) (Nototheniidae)					Reef fishes of the same family or functional group can exhibit strong selectivity for particular reef algae, and thus their grazing effect on the reef community may differ (Mantyka and Bellwood 2007) Selective grazing on *Ulva* by the abundant blenny *Scartichthys* in the Chilean rocky intertidal impacts overall community structure (Ojeda and Muñoz 1999) *Notothenia* feeds selectively on some of the available seaweeds in Antarctica, depending to ~40% on algal diet overall (Iken et al. 1997)
Reptiles (Iguana)	Biting Tearing	Macrograzers	Generalists	Tropical systems	The marine iguana *Amblyrhynchus* in the Galapagos feeds on intertidal and subtidal seaweeds, with algal abundance- and temperature-dependent feeding rates to optimize food intake (Shepherd and Hawkes 2005)
(Green turtle)	Biting Tearing	Macrograzers	Generalists	Tropical systems	Green turtles mostly feed on seagrasses but also consume significant portions of seaweeds, possibly selectively; on an individual basis they may even specialize on an algal over seagrass diet (reviewed in Bjorndal 1997)
Sirenians	Biting Tearing Browsing	Macrograzers	Generalists	Tropical systems	Dugongs feed mostly on seagrasses but can consume considerable amounts of seaweeds either opportunistically or more targeted when seagrass diet is sparse (Whiting 2002)
Birds	Tearing Browsing	Macrograzers	Generalists	Temperate and tropical systems	Brent geese grazing can significantly deplete green algal biomass but has little long-term effects on these fast-growing algae (Rowcliffe et al. 2001)

Second, grazers can be separated by size, with a main separation between meso- and macrograzers (Table 8.1); virtually nothing is known about the impact of the smallest group, micrograzers (<0.1 cm), on seaweeds. Mesograzers are small (mostly 0.1–2.5 cm), and can include juveniles of some larger species, with typically small spatial feeding ranges (Hay et al. 1987; Arrontes 1999). Mesograzers can occur in very high densities on their hosts and their grazing effects are often specific to the algal host rather than the entire seaweed community. Conversely, macrograzers are larger (>2.5 cm) with intermediate to large feeding ranges. The voracious feeding activity of some macrograzers can denude large seaweed stands and consequently influence overall community structure.

A third way of classifying grazers is by their diet specificity, distinguishing specialists feeding on one or few seaweed species from generalists feeding on a large variety of seaweed species and types (Table 8.1). Most marine herbivores tend to be generalists, and many also incidentally ingest some animal material. Feeding selectivity can be driven by a number of factors, among others predation pressure on the herbivore. For example, small, sedentary amphipod mesograzers can specialize to live and feed on chemically defended seaweeds to gain protection against predators (Hay et al. 1989a, b). Food selection can also be driven by the nutritional content of the seaweed. Some crustaceans have higher reproductive fitness when feeding on mixed algal species or on higher quality species (Hemmi and Jormalainen 2002). Specialization of herbivores on a single or few select algal species can also be due to the structural habitat an alga provides the herbivore. For example, the isopod *Idotea baltica* prefers feeding on phlorotannin-rich seaweeds although this causes reduced growth rates, likely because the stable habitat structure of these algae affords protection from predators (Jormalainen et al. 2001a).

8.2 Digestive Adaptations in Grazers

One of the “problems” of seaweed food is its low nutritional quality and the restricted digestibility and assimilation (Montgomery and Gerking 1980). Seaweeds have a high structural carbohydrate content with limited enzymatic digestibility by herbivores, low nitrogen content compared to animal diet, tough tissues, and sometimes metabolites that reduce digestion (e.g., phlorotannins; Targett and Arnold 2001; Amsler and Fairhead 2006). Hence, while seaweeds are often relatively easy to acquire as food because of their abundance and stationary distribution, processing large amounts of algal food to satisfy metabolic needs of the grazer poses many challenges. Digestion and assimilation of seaweeds are best, albeit incompletely, known for herbivorous fishes (for reviews, see Horn 1989; Clements et al. 2009). Adaptations in fishes often include a gizzard or other grinding mechanism and/or acidic stomach environment to mechanically break up and/or chemically lyse the food. They also typically possess a long alimentary tract to optimize assimilatory surface area and gut retention time, and hindgut fermentation of complex carbohydrates through microorganisms. Some of these gut features may not occur at all in some species and can be compensated for by strong expression of the other characteristics. For example, high enzymatic activity compensates for a short, stomachless, alkaline digestive tract in the silverside *Atherinops affinis* (Horn et al. 2006). Much less is known about the physiological processes associated with digestion and assimilation in invertebrate herbivores feeding on seaweeds (Targett and Arnold 2001). Many invertebrate guts contain an array of proteinase, amylase, and lipase enzymes. Similar to herbivorous fishes, microflora is supposed to assist with carbohydrate polymer breakdown, while algal lysis with gut acids may be a less likely mechanism in invertebrate herbivores. The field of seaweed digestion by invertebrate herbivores still requires much research so that ecological and evolutionary frameworks of grazer–macroalgal interactions can be more fully developed.

8.3 Grazer Impacts on Seaweeds and Seaweed Communities

Macrograzer feeding can remove large amounts of seaweed biomass, with strong ecosystem-wide effects such as trophic cascades best known from temperate kelp forests and tropical coral reefs (Pinnegar et al. 2000). Sea urchin grazing on kelps can be one cause for phase shifts from kelp beds with an abundance of kelps, other fleshy algae, and associated invertebrates and fishes to an urchin barren state, where few seaweeds except for encrusting corallines prevail (Steneck et al. 2002). For example, in the Alaskan Aleutian Islands, these phase shifts are closely linked to the presence/absence of sea otters, the keystone species that preys on urchin grazers (Estes and Duggins 1995). Under reduced predation pressure in the absence of sea otters, urchins grow unchecked and overgraze the kelp, causing urchin barrens. The barren phase is stable over long time periods, until a major disturbance, e.g., reintroduction of a predator or disease, reduces sea urchin numbers and kelps can grow back into stable kelp beds. Besides the indirect benefits to kelp forests of sea otter predation on urchins, it also provides positive feedbacks for the otters, which will find more nutritious prey in the complex kelp forests. Trophic cascades including grazing by urchins and/or herbivorous fishes also are well documented in tropical coral reef community shifts between coral-dominated and seaweed-dominated phases (Mumby et al. 2006). Grazing removes seaweeds from coral reefs, thus facilitating space for coral growth and recruitment. When grazing is reduced, such as after the mass die-off of the urchin *Diadema antillarum* in the Caribbean in 1983 (Carpenter 1990) or by overfishing, competitively dominant seaweeds smother corals and dominate the reef community (see Chap. 16 by Mejia et al.). A greater diversity of reef grazers is typically more effective in removing algal biomass, thus increasing overall coral reef resilience (e.g., Duffy et al. 2003).

The feeding activity of small mesograzers is typically nonlethal to large seaweeds, but their grazing activity can still affect host fitness (e.g., reduce growth and reproductive output), and influence overall community structure (Arrontes 1999). The overall community effects of algal biomass removal by mesograzers

Table 8.2 Mesograzer effects on macroalgae and macroalgal communities

Grazing effect	Selected example
No effect on macroalgal growth	At natural abundances, amphipod grazers do not reduce growth in *Sargassum* in Australia (Poore et al. 2009)
Reduction of macroalgal growth	Limpets limit macroalgal growth on exposed rocky intertidal shores throughout Europe, with overall stronger grazing effects on macroalgal abundance as well as spatial variability in assemblages in the north than the south (Coleman et al. 2006)
Reduction of macroalgal reproduction	Selective grazing of periwinkles on meristematic tissue reduces growth and reproduction in the rockweed *Fucus* (Van Alstyne 1990)
Removal of propagules	Mesoherbivores are effective in controlling bloom-forming *Ulva* (as *Enteromorpha*) in the Baltic Sea by grazing on early life-stage propagules (Lotze and Worm 2000)
Algal distribution patterns	Limpet grazing controls seaweed growth at mid-intertidal levels in rocky shores in Spain (Arrontes et al. 2004), but periwinkles do not have the same effect in Sweden (Lindegarth et al. 2001)
Selective grazing	Selective grazing on annual seaweeds in the Baltic Sea releases long-lived fucoids from interspecific competition and maintains overall complex communities (Worm et al. 1999)
Damage to macroalgal tissue causes secondary effects	Grazing of the small gastropod *Lacuna vincta* weakens tissue in the kelp *Nereocystis luetkeana* resulting in increased breaking and mortality through hydrodynamics (Duggins et al. 2001)
Importance of herbivore diversity	Higher diversity of grazers removes more algal epiphytes from seagrasses than similar herbivore abundances of lesser diversity, with additional indirect effects such as increased secondary production in the system (Duffy et al. 2003)
	Diversity and productivity of rocky intertidal algal communities is not linearly related to gastropod grazer diversity, but different grazer species have idiosyncratic effects (O'Connor and Crowe 2005)
Importance of herbivore identity	Selective grazing of different species of herbivorous reef fishes causes different impacts on the algal community, which can also vary depending on the successional stage of the algal community (Burkpile and Hay 2010)
Importance of herbivore life stage and gender	In situ feeding of male and female *Idotea* isopods on *Fucus* differs with males preferring apical portions and females preferring the less nutritious but better protected basal portions of the algae, likely as a risk avoidance strategy (Jormalainen et al. 2001b)

are dependent on many complex interactions. These include feeding rate and mode of the dominant grazer, growth rates of the algae, competitive interactions with and among other community members, as well as interactive effects with the physical environment (Hawkins and Hartnoll 1983; Coleman et al. 2006; Jenkins et al. 2008; see Table 8.2 for examples for the following effects). Even if mesograzer consumption of adult seaweeds is negligible, strong community-structuring effects may occur in the case of selective removal of algal propagules. Selective grazing reduces seaweed interspecific competition, influencing overall community composition and algal distribution patterns. Mesograzing at high densities can damage valuable parts of the algal thallus such as reproductive or meristematic regions, facilitate access for other grazers or pathogens, or weaken the thallus and render the seaweed prone to breakage. Seaweed biomass reduction may be greater with increased herbivore diversity, in addition to high abundance, because the complementary feeding modes and preferences of different grazers are more effective in removing algal biomass (Table 8.2). Conversely, while there is little directed research yet, meta-analysis indicates that higher algal diversity may lead to decreased grazer effects (Hillebrand and Cardinale 2004). It was argued that, if more algal species are present, there is a higher likelihood that the community contains unpalatable species, or that a more diverse system may have increased indirect and facilitative effects that may benefit seaweeds overall (Hillebrand and Cardinale 2004). Similar to macrograzers, mesograzers themselves are often under strong control of predators, which can efficiently decimate grazer densities and thus indirectly enhance seaweed growth. For example, micro-carnivorous fishes efficiently prey upon mesograzers in a Californian kelp bed and enhance kelp frond density (Davenport and Anderson 2007).

Among other environmental variables, mesograzers may be particularly susceptible to hydrodynamic forces that can dislodge them from their host alga, thus reducing the effects that grazing has on seaweed communities. Nutrient levels, e.g., due to eutrophication in coastal waters (“bottom-up” effects), may partially counteract grazer-induced “top-down” effects on seaweed diversity and production. The relative importance of grazer versus nutrient effects on seaweed communities is highly context dependent; nutrient effects seem to be strongest in naturally high-nutrient systems but less important in oligotrophic systems, and they may also vary based on algal functional group (e.g., foliose, filamentous, crustose; Burkpile and Hay 2006).

Occasionally, herbivore feeding can also benefit seaweeds and communities (Hay et al. 2004). A common effect of mesograzers is the removal of filamentous epiphytes from a host, possibly affording better light and nutrient acquisition to the host plant by reducing algal epiphyte biomass (Duffy 1990). Also, coralline algae have higher accretion rates when grazed because the positive effects of grazing, such as the removal of competitively superior fleshy algae, outweigh the grazing damage to the coralline (Littler et al. 1995). Grazing, in general, cannot only open new space for algal recruits, but in the case of grazing gastropods, the pedal mucus trail left on the rocky surface can effectively trap spores and other seaweed propagules and support their germination (Santelices and Bobadilla 1996). Considering the typically high abundance of gastropods in rocky intertidal systems, this may enhance new seaweed recruitment (and new food resources for the grazer!) into an area where seaweeds are under strong grazing pressure. Grazing may also enhance algal productivity and algal recruitment even if algal biomass is reduced. For example, it has been hypothesized that either the reduction of self-shading or the increase in nutrients from herbivore excretions may have positive effects on seaweed productivity (Carpenter 1986). Lastly, the preferential feeding of amphipods on reproductive algal tissue can lead to an increased release and recruitment of spores (Buschmann and Vergara 1993).

8.4 Seaweed Defenses Against Grazing

Algal defenses against herbivores present the other side of the coin in grazer–seaweed interactions, where defenses presumably have developed in response to selective pressures of grazers. The large array of algal defense mechanisms ranges from tolerance and fast replacement of lost tissue, to temporal and spatial escapes, to structural and chemical defenses. Several different defense strategies may be employed simultaneously in some seaweeds, and many of these defenses may also have functions other than herbivore deterrence (e.g., antifouling, antimicrobial defense, allelopathic functions). These defenses are commonly distinguished as non-coexistence and coexistence strategies, with the latter encompassing structural and chemical defenses (e.g., Lubchenco and Gaines 1981; Duffy and Hay 1990; Table 8.3).

In non-coexistence strategies the encounter of seaweeds with herbivores is minimized. These "strategies" do not imply a specific, directed behavioral response in seaweeds but likely are a result of chance or are evolutionary developments from situations where spatial and temporal occurrence of seaweeds coincided with minimal herbivore activity. Overall, grazing pressure is variable over time and space, and seaweeds can escape grazing by occurring in places, or by completing important life history phases such as initial growth or reproduction during times, where and when herbivores are not present or active. These strategies are most effective at driving co-evolution in systems where temporal and spatial distribution of herbivores is predictable. Escape in size occurs when seaweeds outgrow the sporeling stage as a bottleneck of high grazer susceptibility and reach a size where they are unaffected by the specific feeding mode of the abundant herbivore. Lastly, macroalgae also can escape herbivores by association with other organisms that provide them chemical or structural protection from grazers (for examples of the above see Table 8.3).

Coexistence strategies lower the herbivore's attraction to a seaweed because of specific structural or chemical traits of the alga. The most common example of structural defenses, also referred to as mechanical or morphological defenses, involves the inclusion of calcium carbonate into algal cells (Paul and Hay 1986). In their functional-form model, Steneck and Watling (1982) suggest that calcareous seaweeds, specifically crustose coralline forms, have the highest grazer resistance of all algal forms, and grazing on calcareous forms requires specialized mouthparts in the herbivore. The main herbivores able to graze on coralline algae are chitons, limpets, sea urchins, and parrot fishes. Coralline algae often are abundant despite high herbivore densities, demonstrating that herbivore damage is minimal.

Table 8.3 Algal defenses against grazing

Defense mechanism	Selected example
Non-coexistence strategies	
Escape in time	The highly palatable green alga *Ulva* forms early spring blooms from an overwintering propagule bank in the Baltic Sea, thus avoiding intense herbivore pressure, which efficiently suppresses *Ulva* later in the season (Lotze et al. 2000)
Escape in space	Turf algae on the Great Barrier Reef thrive in regions of reduced herbivory, but are readily consumed when transplanted to regions of high herbivore abundance (Bonaldo and Bellwood 2010)
Escape in size	The chiton *Katharina* is very effective in removing new recruits of the low intertidal kelp *Hedophyllum* in the Northeast Pacific but does not graze on the adults (Markel and DeWreede 1998)
Associational defense	The palatable red alga *Gracilaria* is protected from sea urchin grazing when it occurs associated with the unpalatable brown alga, *Sargassum,* in the temperate Atlantic (Pfister and Hay 1988) In tropical coral reefs, seaweeds persist even under high herbivore abundances when they are covered with epiphytic cyanobacteria (Fong et al. 2006)
Coexistence strategies	
Structural defense	*Fucus* produces adventitious branches after grazing damage, which act as structural defenses against further grazing, although high phlorotannin content in these branches may also present a chemical defense (Van Alstyne 1989) *Padina* on coral reefs exhibit morphological plasticity with an erect, foliose morphology in the absence of grazers and a more resistant turf morphology under high grazing pressure (Lewis et al. 1987)
Chemical defense	
Tropical systems	A large variety of green, red, and brown seaweeds deter feeding in many invertebrate and vertebrate grazers using a rich arsenal of terpene and acetogenin metabolites (see Table 2.1 in Pereira and da Gama 2008). For example, the Brazilian brown alga *Stypopodium zonale* (Dictyotales) produces a diterpene mixture that chemically differs depending on location, and some compounds of the mix deter urchin and crab feeding more than others (Soares et al. 2003)
Temperate systems	While generally less rich in natural products active against grazers than tropical algae, temperate seaweeds are often chemically defended, with phlorotannins in brown algae being the most-studied group (Jormalainen and Honkanen 2008). However, phlorotannins are not always the deterrent compound; in *Fucus vesiculosus*, a galactolipid and uncharacterized non-phenolic compounds are active in deterring an urchin grazer (Deal et al. 2003)
Polar systems	Extracts of 20 macroalgae along the Western Antarctic Peninsula deter sympatric grazers, although responsible compounds are often unidentified (Amsler et al. 2005). Phlorotannins are abundant in most of the dominant brown algae and some deter feeding in sea star, amphipod, and/or fish grazers (Iken et al. 2007, 2011)

Many coralline algae also contain defensive chemicals in addition to calcification. For example, chemical defenses instead of calcification were the driving mechanism for reduced grazing of urchins, amphipods, and parrot fishes on the tropical coralline green algae, *Rhipocephalus* and *Udotea* (Hay et al. 1994). Calcification in seaweeds can also be paired with additional non-coexistence (avoidance) strategies. One example is the tropical green coralline alga *Halimeda*, which produces new, non-calcified segments only at night when herbivorous reef fishes are inactive (Hay et al. 1988). The price for herbivore resistance of calcareous seaweeds is very low growth rates, which prevent coralline algae from easily replacing tissue that is lost through grazing. A different example of structural defense is referred to as bet hedging and can occur in heteromorphic seaweeds. Here, a fleshy, upright form has high photosynthetic and growth rates but is susceptible to grazers, while a crustose form is more grazer resistant at the expense of reduced growth rates (e.g., Slocum 1980). With this strategy, the crustose form prevails in situations of high grazer abundance while the upright form occurs when herbivores are fewer or absent. Another type of structural (mechanical) defense is where water motion creates a whiplash effect of some kelps, which will prevent urchins from entering kelp beds to graze (Konar 2000).

Coexistence strategies using chemical defenses are probably the best-studied area of seaweed defenses against herbivores, and a recent book provides an excellent review of the topic (Amsler 2008). These defenses also are covered from a mechanistic perspective in Chap. 9 by Amsler, while they are viewed in this chapter from a strategic and community perspective. Marine seaweeds from all latitudinal ranges and ecosystem types produce a wide variety of secondary metabolites that function as herbivore deterrents (Maschek and Baker 2008; see Table 8.3 for examples from different latitudinal systems). These chemical defenses mostly reduce the palatability or nutritional quality of the seaweed, or can also reduce the fitness and survivorship of the herbivore through toxic effects. The functions and mechanisms of the multitude of defensive chemical metabolites have evoked a number of predictive models. Many of these models are based on the assumption that the production, storage, or degradation of defensive metabolites is costly, and that implementation of defenses is thus under regulation to optimize energy use in seaweeds (Pavia and Toth 2008). Models of seaweed chemical defenses that are mostly based on resource availability are reviewed elsewhere in detail (Cronin 2001; Amsler and Fairhead 2006; Pavia and Toth 2008). One model, the Optimal Defense Theory (ODT; Rhoades 1979), is specifically based on herbivory as the selective driver of defensive strategies. The ODT predicts that allocation of defensive compounds to specific parts within the alga is in direct proportion to the value of the thallus part for the seaweed's fitness as well as to the risk of attack, and in inverse relation to the cost of defense production. Within the framework of the ODT, induction of these defenses should occur during times when the risk of herbivore attack is greatest and unpredictably variable. The preferential allocation of defensive chemicals and induction of defenses after initial damage in seaweeds has been abundantly tested and reported in the literature and much, although not unanimous, support has been found (see Toth and Pavia 2007 for review). In part the debate about differential defense allocation to the most valuable thallus parts may be hampered by the definition of "valuable." One particularly well-studied system of the ODT is phlorotannin allocation in brown algae, even though the defensive role of phlorotannins has been controversial and seems to be context-dependent on herbivore and environment (Amsler and Fairhead 2006). Using sensitivity analysis, which determines the relative contribution of different life processes to overall population growth, Pavia et al. (2002) related life processes to different thallus parts in the fucoid *Ascophyllum nodosum*, and thus determined fitness values of different thallus parts. Phlorotannin concentrations and resistance to gastropod grazers were positively correlated to these fitness values in accordance to the ODT.

8.5 Effects of Seaweed Chemical Defenses on Herbivores and Communities

Algal chemical defenses can indirectly influence herbivore populations by affecting their overall food consumption and lead to reduced growth or reproduction. Metabolites can also directly affect herbivore survival, although practical separation of indirect and direct effects is often difficult. Phlorotannins, common metabolites in brown algae, have the potential to bind to digestive enzymes as well as with plant nutrients and thus limit assimilation efficiencies in the grazer (Targett and Arnold 2001). For example, the assimilation efficiency in fishes was greatly reduced when feeding on a phlorotannin-rich diet (Boettcher and Targett 1993), and egg production in periwinkles was reduced by phlorotannins (Toth et al. 2005). Similarly, the terpenoid metabolites produced by the brown alga *Dictyota* significantly reduced growth, survival, and reproduction in some grazing amphipods (Cruz-Rivera and Hay 2003). These fitness effects can depend on metabolite concentration and on the specific herbivore species, as there is considerable variation in the effects of the same algal metabolite on even closely related herbivores. Conversely, some mesograzer populations can ultimately benefit from seaweed defenses by gaining protection from predators when living associated with a chemically defended host, even if this comes with reduced fitness as a trade-off (Hay et al. 1988, 1989a, b).

Relatively little understanding exists on the structuring role of seaweed chemical defenses on overall communities beyond the specific interactions between a particular seaweed and herbivore (Hay 2009). Chemically well-defended seaweeds can be very abundant and even dominate communities, independent of latitude or algal group; this attests to the competitive advantage chemical defenses may provide. On tropical reefs in Brazil with high grazing pressure, members of the tropical green algae *Bryopsis* and *Caulerpa,* the red alga *Laurencia,* and the brown alga *Dictyota* chemically deter herbivore grazing and also are highly abundant (Marques et al. 2006; Villaça et al. 2010). *Fucus vesiculosus* is the dominant habitat-providing seaweed along rocky shores in the Baltic Sea, and phlorotannins act as effective defenses in the adult seaweed against most grazers (Jormalainen and Honkanen 2008). Antarctic shallow waters are dominated by large brown algae of the order Desmarestiales, which are unpalatable to most sympatric grazers. In some cases, this may be due to relatively high phlorotannin contents (Amsler et al. 2005; Iken et al. 2011). Chemical defenses in seaweeds may also play a role in the invasive potential of a species, which typically have significant effects on the structure and biodiversity of the native community. For example, the invasive, chemically defended *Caulerpa taxifolia* is largely unpalatable and presents poor habitat to a variety of native grazers in temperate Australia, making it unlikely that grazing could control the abundance or spreading of the invasive species (Gollan and Wright 2006). Chemical defense in seaweeds also can have community-wide effects by altering trophic dynamics, and can even change the outcome of trophic cascades. In Australia, the chemically defended red alga *Delisea pulchra* survived intense urchin grazing in a kelp bed, which led to an intermediate stable community state containing grazer-resistant foliose algae between the typical alternate states of kelp beds and urchin barrens (Wright et al. 2005). Waterborne cues released by herbivores grazing on macroalgae may function as a form of chemical communication with neighboring con-specific algae to increase their defense levels (Toth and Pavia 2007). However, these cues may act in a broader sense as "infochemicals" when signaling to other community members. Cues released from herbivore-algal grazing may attract potential predators of the herbivores, which would benefit the seaweed. Both a fish and a crab predator were significantly attracted to cues released by *Ascophyllum nodosum* when grazed by periwinkles, thus inducing top-down control of the herbivore by the two predators (Coleman et al. 2007). This shows that such waterborne cues may act as a seaweed distress signal, a mechanism well known from terrestrial plant–insect interactions (Dicke 2009). In a different example, cues exuded by the chemically defended *Delisea pulchra* in Australian kelp beds induced settlement of urchin larvae, although the chemically defended alga is unpalatable to the adult urchins (Williamson et al. 2004). Adult urchins will instead feed on other seaweeds within the community, thus providing a competitive advantage to *D. pulchra.* Simultaneously, urchins gain associational protection against fish predators from the chemically defended alga in their habitat.

8.6 Climate Change Effects on Seaweed–Herbivore Interactions

An emerging, yet timely, consideration is the effects that climatic changes will have on the interactions between seaweeds and grazers. Metabolic theory predicts rising temperatures to generally increase metabolic rates in both seaweeds and herbivores (see also Chap. 3 by Eggert and Chap. 18 by Bartsch et al.). Manipulative tank experiments, however, indicated that temperature rise has a proportionally larger effect on grazers, which outweigh any increased algal growth. This resulted in an overall reduction of algal biomass (O'Connor 2009). Conversely, no change in herbivore impact at higher temperatures was seen in an in situ experiment in a rocky intertidal in California (Morelissen and Harley 2007). It was hypothesized that multiple abiotic drivers interacted with varying effects on biotic interactions, partially offsetting and ameliorating each other, thus not leading to a clearly detectable temperature effect. It is yet uncertain how simultaneous changes in light and nutrient regimes with temperature increases would influence seaweed–grazer relationships. But it seems that any climate-driven temperature effects on species-specific seaweed–grazer interactions may not propagate linearly through the food web, and depend, among others, on the body size, diversity, diet specificity, and connectivity of members of the food web (Petchey et al. 2010; see also Chap. 19 by Roleda and Hurd).

The seaweed–grazer effects of other variables subject to global change, such as sedimentation or ocean pH, are poorly understood. Many coastal regions experience an increase in sedimentation, mostly due to coastal erosion and, in cold-temperate and polar regions, the increased melting of glaciers (Bogen and Bønsnes 2003). Regions under strong sediment influence are characterized by lowered seaweed and invertebrate density and diversity (Spurkland and Iken 2011). How this translates into specific effects on seaweed–herbivore interactions is not yet known. Similarly, it is known that increased ocean acidification reduces the abundance and fitness of crustose coralline algae on coral reefs and may enhance fleshy algal growth, but the specific impacts of pH on grazers and on seaweed–grazer relationships are unknown (Kuffner et al. 2008).

8.7 Conclusions

Despite the many advances achieved in the broad field of grazer–seaweed interactions, many if not most topics require more comprehensive investigation to reach a more complete understanding. Generalizations made on patterns or interactions between grazers and seaweeds are often based on few individual studies and need to be more thoroughly tested with different species and at multiple locations. This will allow us to better understand the variability of individual patterns within a (possibly) general concept. Obviously, globally occurring changes in climate and ocean chemistry are likely to have effects on the seaweed–grazer systems as we have started to understand them so far. Aside from metabolic changes in both grazers and seaweeds, marine systems are expected to undergo “functional homogenization,” where numerous specialist species fulfilling various functions are replaced with few generalist species assuming most ecosystem functions (Clavel et al. 2011). This homogenization will inevitably have important effects on the often species-specific nuances in seaweed–grazer interactions, evoking important questions of the role of the diversity of these myriad interactions in ecosystem resiliency and functioning.

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Chapter 9
Chemical Ecology of Seaweeds

Charles D. Amsler

9.1 Overview

Chemical ecology is the study of chemically mediated interactions between organisms or between organisms and their environment. It is convenient to separate these interactions into sensory chemical ecology and defensive chemical ecology. However, sensory and defensive chemical interactions cannot always be separated as waterborne signals released by seaweeds under attack by herbivores can be sensed by neighboring algae and induce a defensive response in the unattacked neighbors (Toth and Pavia 2000). Moreover, seaweed defenses against biofouling can function by interfering with chemical communication between bacteria on the algal surface (Kjelleberg et al. 1997).

Sensory chemical ecology can be subdivided into chemical communications between organisms, be they intentional or not, and sensing and responding to the abiotic chemical environment of the alga. There is a large body of literature on seaweeds sensing and physiologically responding to their nutrient environment (see Chap. 4 by Gordillo). However, in practice such studies have been outside the scope of "chemical ecology" and this chapter follows the more narrow definition, which does not include physiological responses to nutrients.

Defensive chemical ecology can likewise be subdivided, often by what is being defended against. Most studies of seaweed chemical ecology as a whole involve studies of defenses against predation, which from a mechanistic perspective are an important focus of this chapter. They are discussed with respect to community impacts in Chap. 8 by Iken. Chemical defenses can also be produced in response to organisms that grow on or over seaweeds, referred to as *biofoulers* or *epibionts*, to pathogenic organisms, and to competitors. Production of chemical defenses against competitors is commonly referred to as *allelopathy*. These categories are not

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clear-cut as biofoulers may also have characteristics of pathogens or competitors, and individual defensive metabolites may have multiple defensive roles (e.g., Schmitt et al. 1995).

It would be impossible to comprehensively review seaweed chemical ecology in a short chapter such as this. Indeed there is a recent book devoted entirely to algal chemical ecology (Amsler 2008a) and it could not be comprehensive with respect to most subjects. Rather, I have attempted to highlight studies that illustrate the various aspects of seaweed chemical ecology while providing references to more detailed reviews.

9.2 Sensory Chemical Ecology

9.2.1 Chemical Communication

Chemical communication is important in sexual reproduction of brown seaweeds. This has received a great deal of research attention and been the subject of numerous reviews (e.g., Maier and Müller 1986; Maier 1995; Amsler and Iken 2001; Pohnert and Boland 2002; Amsler and Fairhead 2006). Comparatively, virtually nothing is known about such phenomena in green or red seaweeds although similar mechanisms are well documented in some freshwater and microscopic green algae (Sekimoto 2005; Amsler 2008b).

Brown seaweeds utilize pheromones released by female gametes both as male gamete attractants and, in some taxa, for stimulating the release of male gametes. Although this behavioral attraction was first observed in the 1800s, the specific pheromones responsible did not begin to be identified until the 1960s (cf. Amsler and Fairhead 2006). The 12 known pheromones from over 60 brown algal species in 13 orders are all C_8 or C_{11} hydrocarbons or epoxides (Maier 1995; Pohnert and Boland 2002). These diffuse rapidly away from the female gametes and the range at which perception by males is possible has been estimated at up to several millimeters (Maier and Müller 1986).

Gamete attraction in brown algae is probably best understood in *Ectocarpus siliculosus*, where a responsible pheromone was first identified (Müller 1967, 1968). Upon settlement, female gametes secrete the C_{11} pheromones ectocarpene and pre-ectocarpene (Müller 1978; Pohnert and Boland 2002), which cause a complex response in male gametes that has been described as a chemo-thigmo-klinokinesis [reviewed by Maier and Müller (1986) and Müller (1989)]. Upon sensing the pheromone, the male gametes remain in contact with a surface (the “thigmo” component) and slow down. As the pheromone concentration increases, the gametes make sharp, nearly U-turns more and more frequently (hence a “chemokinetic” response; cf. Amsler and Iken 2001) and thereby are effectively trapped in the area of the female gamete until they contact it. In contrast, male gametes of the kelp *Laminaria digitata* are able to swim directly toward female gametes releasing the C_{11} pheromone lamoxirene [reviewed by Maier and Müller (1986) and Müller (1989)], a behavior that can be described as a true chemotaxis (cf. Amsler and Iken 2001). Lamoxirene also stimulates release of male gametes from male gametophytes' antheridia (Maier 1982).

Unintentional forms of chemical communication, at least from the perspective of the signal sender, occur between spores of the green seaweed *Ulva* spp. and biofilm bacteria as well as in bacterial stimulation of spore release of the red alga *Acrochaetium* sp. (see also Chap. 11 by Potin and Chap. 10 by Friedrich). It has been known for some time that biofilm composition can influence *Ulva* spore settlement (e.g., Thomas and Allsopp 1983) and that bacterial metabolites are necessary for normal development of *Ulva* germlings (e.g., Provasoli and Pinter 1980). Joint et al. (2000) reported that within biofilms, the spores preferentially settle on or next to bacterial cells. This settlement pattern is the result of spores "eavesdropping" on *N*-acylhomoserine lactone (AHL) signals (Joint et al. 2002; Tait et al. 2005) which are produced by many bacteria for quorum sensing, an intraspecific form of chemical communication involved in multiple bacterial processes (Chhabra et al. 2005). The mechanism is a form of chemokinesis in which the spores drastically reduce their swimming speed when close to the AHL source, but this only occurs if they are in contact with the surface of the substrate (Wheeler et al. 2006).

AHLs can also be involved in seaweed spore release. The filamentous red alga *Acrochaetium* sp. is a common epiphyte on the larger red seaweed *Gracilaria chilensis* and spore release in *Acrochaetium* sp. appears to be induced by AHLs from bacteria growing epiphytically on *G. chilensis* (Weinberger et al. 2007; see also Chap. 11 by Potin). However, no such effect of AHLs was observed with another (although not closely related) filamentous red alga, *Sahlingia subintegra*, which also grows epiphytically on *G. chilensis* (Weinberger et al. 2007).

As discussed later, some seaweeds release waterborne chemical cues when under attack by some (but not all) herbivores. These cue adjacent conspecifics to induce the production of defensive chemical compounds even without being attacked themselves (Toth and Pavia 2000; Toth 2007). Predators of herbivorous snails preying on the seaweeds can also sense these cues, another example of communication between species. Coleman et al. (2007a) reported that fish predators can be attracted by the scent of snails feeding on other organisms but significantly more so if the snails are grazing on *Ascophyllum nodosum*, an alga known to induce its own defenses when neighboring conspecifics are under attack (Toth and Pavia 2000). Crab predators of the snails were attracted by *A. nodosum* that had been grazed by snails even if the snails had been removed (Coleman et al. 2007a).

9.2.2 Environmental Sensing

Seaweed spores are known to respond to physiochemical cues, in particular to surface hydrophobicity. Spores from several species of brown and green algae settle preferentially on hydrophobic surfaces in the laboratory, although the adaptive significance of this in the context of the biofilm environments they settle within in nature is unknown (Amsler 2008b). Interestingly, although *Ulva* spores given the choice between alternating hydrophobic and hydrophilic surfaces settle preferentially on the hydrophobic patches (Callow et al. 2000), when presented with a hydrophobicity gradient they settle more in hydrophilic regions (Chaudhury et al. 2006). In the brown alga *Hincksia irregularis*, surface hydrophobicity interacts with light and light gradients (Greer and Amsler 2002, 2004) and with potential antifouling compounds (Greer et al. 2003) to influence spore settlement patterns.

Some brown algal spores respond to inorganic nutrients in their swimming and settlement behaviors. Spores from several species of kelps (Order Laminariales) demonstrate chemotactic swimming responses toward or away from nutrients (Amsler and Neushul 1989; Fukuhara et al. 2002). Spores themselves probably have no need for inorganic nutrients, but the filamentous gametophyte stage into which they germinate after settlement certainly does. Because these gametophytes are microscopic and confined to the biofilm environment the spore settles in, the nutrient microenvironment in which they settle likely has a profound influence on the ultimate growth and reproduction of the gametophyte. *Macrocystis pyrifera* spores are attracted to ammonia concentrations which stimulate gametophytic growth but not to high concentrations which inhibit it (Amsler and Neushul 1989). The spores are also attracted to low concentrations of iron which stimulate gametophytic reproduction, but not to higher, inhibitory concentrations (Amsler and Neushul 1989). Independent of chemical gradients, and apparently via a somewhat different sensory mechanism, kelp spores also settle more rapidly in the presence of nutrients which are necessary for gametophytic growth and reproduction (Amsler and Neushul 1990).

9.3 Chemical Defense

9.3.1 Defenses Against Predation

Seaweed chemical defenses against herbivores have received the bulk of attention in seaweed chemical ecology. They have been the subject in whole or large part of numerous recent reviews appearing in journals (e.g., Pohnert 2004; Amsler and Fairhead 2006; Ianora et al. 2006; Amsler et al. 2009b; Paul et al. 2011) and in six chapters of a recent book (Amsler 2008a). They are also discussed in Chap. 8 by Iken, particularly with respect to their population or community level importance. This section focuses on selected sets of studies which illustrate defenses from a more mechanistic perspective.

Seaweeds utilize a variety of chemical compounds for defense (Maschek and Baker 2008) and these may be spread throughout the alga or be localized to particular parts of the thallus (Jormalainen and Honkanen 2008). Chemical defenses can be produced constitutively, only when a seaweed is attacked by a herbivore, or some combination thereof. Defenses synthesized only when under attack or in greater amounts when under attack are referred to as *induced defenses*. Alternatively, some defenses, known as *activated defenses*, are produced constitutively but in an inactive or less toxic form and are rapidly changed into the bioactive form upon herbivore attack. There are a number of theories based on terrestrial plants (Stamp 2003; Agrawal 2007) that have been used for predictions of what kinds of defensive compounds seaweeds should produce as well as when and where they should make them. These ideas were recently reviewed by Amsler and Fairhead (2006) and Pavia and Toth (2008).

The red alga *Delisea pulchra* is a well-studied example of constitutive chemical defenses against predation (and against biofoulers, see also Chap. 8 by Iken, Chap. 11 by Potin). *D. pulchra* elaborates a number of halogenated polyketide metabolites known as *furanones* (de Nys et al. 1993) which deter grazing by many, but not all, herbivores (Wright et al. 2004). Interspecific variations in furanone levels are heritable (Wright et al. 2004) and have a cost to the seaweeds in terms of reduced growth and fecundity under some circumstances (Dworjanyn et al. 2006a). That defensive levels vary within a species, are heritable, and come at a cost to the producing organism are assumptions underlying chemical defense theories (Stamp 2003; Agrawal 2007). However, they are rarely documented, particularly in seaweeds, making *D. pulchra* a particularly important model.

Constitutive (and other) defenses are also well studied in a number of brown seaweeds, particularly in members of the Orders Fucales and Dictyotales (Amsler and Fairhead 2006). In the Fucales, one important model species has been *Fucus vesiculosus*, particularly from northern Europe where the defensive compounds appear to be phlorotannins, a class of large, phenolic compounds that are widely distributed in brown algae (Amsler and Fairhead 2006; Jormalainen and Honkanen 2008). Phlorotannin levels in these seaweeds have a heritable component and also vary geographically, over time, and with a variety of environmental parameters, which has facilitated tests of a diverse range of ideas in defensive chemical ecology (Jormalainen and Honkanen 2008). Seaweeds in the Dictyotales utilize a variety of smaller compounds for defense with the best studied examples being terpenoids, particularly in the genus *Dictyota* (Pereira and da Gama 2008). These seaweeds have also been used in a wide variety of studies of how defensive chemicals mediate seaweed–herbivore interactions. For example, they have been used to demonstrate that chemical defenses interact with the nutritional quality of an alga to influence not only how much of the alga is consumed by a herbivore, but also the ultimate impact on herbivore fitness (Cruz-Rivera and Hay 2003). They have also been particularly useful in studies of how some herbivores are able to tolerate algal chemical defenses (Hay 2009; Sotka et al. 2009).

Activated chemical defenses are best understood in several green seaweeds including two siphonous genera: *Halimeda* and *Caulerpa*. *Halimeda* spp. constitutively produce the diterpenoid halimedatetraacetate which itself deters fish grazing, but upon wounding the seaweeds rapidly convert it to an even more potent grazing deterrent, halimedatrial (Paul and Van Alstyne 1992). *Caulerpa* spp. produce the sesquiterpene caulerpenyne constitutively but upon wounding rapidly convert it to several more reactive aldehydes (Jung and Pohnert 2001; Jung et al. 2002). Caulerpenyne is deterrent against some but not all herbivores (Jung et al. 2002; Baumgartner et al. 2009) as it significantly reduces food quality due to protein cross-linking. Due to their chemical characteristics, the aldehydes derived from caulerpenyne activation presumably have greater bioactivity but this has been difficult to test because of their instability. Other green algal species, particularly in *Ulva* and related genera, produce high levels of dimethylsulfoniopropionate (DMSP) which has multiple roles in algae (Van Alstyne 2008). Upon wounding, several algae convert DMSP into dimethylsulfide and acrylic acid, both of which are feeding deterrents to sea urchins and likely act as activated defenses (reviewed by Van Alstyne 2008).

Fucoid brown algae have served as important models in understanding induced defenses in seaweeds, particularly *Ascophyllum nodosum* and *Fucus* spp. which elaborate phlorotannins as chemical defenses (Amsler and Fairhead 2006). However, interactions involving induction of defenses vary with species and even population. *A. nodosum* has been shown to increase phlorotannin production and become more unpalatable when under attack by snails but not by isopods (Pavia and Toth 2000) while in some (but not all) populations *Fucus vesiculosus* induces defenses (measured as palatability) when attacked by either snails or isopods (Rohde et al. 2004). Mechanical wounding alone does not induce defenses in *A. nodosum* (Pavia and Toth 2000) and the induction appears to be a response to digestive enzymes present in the snails' saliva (Coleman et al. 2007b). Snails grazing on *A. nodosum* result in waterborne cues being released that enable neighboring *A. nodosum* individuals to induce defenses even in the absence of being wounded themselves (Toth and Pavia 2000) and also can attract predators of the snails (see also Chap. 8 by Iken). In *F. vesiculosus*, waterborne cues resulting in induction of defenses in neighboring individuals are produced in response to predation by isopods but not snails (Rohde et al. 2004). However, although predation by isopods also directly induces defense production in two other species of *Fucus*, in these other species there is no induction from waterborne cues (Rohde and Wahl 2008).

9.3.2 Defenses Against Pathogens

Seaweed pathogens include bacteria, fungi, and filamentous algal endophytes. These relationships and the seaweeds' chemical defenses against pathogens have been the subject of several recent reviews (Weinberger 2007; Lane and Kubanek 2008; Potin 2008; Goecke et al. 2010; see also Chap. 11 by Potin).

One seaweed defense that has been studied with both bacterial and filamentous algal endophyte pathogens is the production of reactive oxygen species (e.g., hydrogen peroxide). These are produced in response to breakdown products from the algal cell walls during pathogen entry (Weinberger 2007; Potin 2008). Such defenses are referred to as *oxidative burst responses*. In some cases, particularly with bacteria, the ability of the reactive oxygen species to oxidize a wide variety of organic molecules may be enough to overcome the pathogen (e.g., Weinberger et al. 2001). In many others, particularly with endophytes, the oxidative burst also triggers a series of activated and induced chemical and structural defenses to contain the infection (Potin 2008).

Many seaweeds have been shown to produce organic compounds that can inhibit growth of bacteria or other pathogens (Bhadury and Wright 2004; Goecke et al. 2010). However, just because an alga makes a compound that can inhibit a pathogen (or biofouling organism) in vitro does not show that it functions as such in nature. To establish that, it is necessary to know that the compound is localized in a way that the pathogen comes into contact with it at a concentration high enough to be effective. This has been shown with defenses against fungal pathogens in several seaweeds. The brown alga *Lobophora variegata*, or more likely a bacterial symbiont of it, produces lobophoralide, a polycyclic macrolide which can be extracted from its surface at concentrations which inhibit the growth of some higher fungi, including seaweed pathogens (Kubanek et al. 2003). The red alga *Callophycus serratus* produces a suite of diterpene-benzoate macrolides and diterpene-alcohols which also inhibit fungal growth (Lane et al. 2009). In the first study of its kind, desorption electrospray ionization mass spectrometry was used to image and quantify these molecules in patches on the seaweed's surface and at concentrations sufficient to inhibit the pathogenic fungi (Lane et al. 2009).

9.3.3 Defenses Against Biofouling

Chemical defenses against biofouling are like those against pathogens in that just because a seaweed produces a compound that can inhibit fouling in vitro, to show ecological relevance against biofouling one must establish that the compound is present at the surface of the alga at a biologically effective concentration (Steinberg and de Nys 2002). Perhaps the most thoroughly studied example of this in seaweeds is the case of halogenated furanones produced by the red alga *Delisea pulchra* as defenses against both predators (see also Chap. 8 by Iken, Chap. 11 by Potin) and biofoulers. These are present at the cell surface at known concentrations (Dworjanyn et al. 1999). They mimic bacterial AHL quorum sensing molecules and interfere with numerous bacterial processes, including attachment, at the concentration range in which they occur on the algal surface (Kjelleberg et al. 1997; Maximilien et al. 1998). They also inhibit the attachment of propagules from four species of fouling macroalgae at surface-level concentrations (Dworjanyn et al. 2006b). Surface extracts of the brown alga *Dictyota menstrualis* have been shown to contain the diterpenoids pachydictyol A and dictyol E, which are also known to defend against herbivores, and algal surface extracts including these compounds inhibited the settlement of larvae of a fouling bryozoan when coated onto artificial surfaces (Schmitt et al. 1995). Surface extracts of the red alga *Bonnemaisonia hamifera* contain a poly-halogenated 2-heptanone at concentrations that inhibit bacterial biofouling (Nylund et al. 2008). The green alga *Ulva reticulata* appears to release a water soluble antifouling defense. Water collected from the vicinity of the seaweeds in nature inhibits attachment of larvae of fouling bryozoans and hydroids (Harder et al. 2004). Some, but not all, of this could be the result of compounds actually produced by a bacterial species colonizing the surface of the algae (Harder et al. 2004).

9.3.4 Allelopathy

Allelopathy (chemical defense against competitors) is relatively widely studied in freshwater systems including in macrophytic algae, vascular plants, and phytoplankton (Gross 2003; see also Chap. 11 by Potin). In marine systems there have been studies showing allelopathic effects of water-soluble compounds from seaweeds on the growth of phytoplankton in laboratory conditions, but the significance of such interactions in natural populations is unclear. On the other hand, seaweeds often compete with other sessile, macroscopic organisms for space (see Chap. 7 by Edwards and Connell) and the advantages of being able to inhibit the growth of such competitors are obvious. There have been at least two studies of such interactions under ecologically relevant conditions. The red alga *Plocamium hamatum* causes tissue necrosis in soft corals upon physical contact due to allelopathic effects of the monoterpene chloromertensene (de Nys et al. 1991). In a study of the effects of contact by multiple seaweed species on two species of hard corals, Rasher and Hay (2010) reported that in nearly half the interactions, seaweeds caused bleaching (loss of symbiotic microalgae) of the corals. This was due to the physiological stress imposed on the microalgal symbionts (measured as photosynthetic efficiency). In nearly every interaction where the intact seaweed caused this effect, so did lipophilic chemical extracts of the seaweed (Rasher and Hay 2010).

9.4 Outlook

If this chapter were about the chemical ecology of terrestrial organisms rather than of seaweeds, the relative lengths of the above sections would be vastly different. Terrestrial chemical ecology is currently dominated by studies of sensory chemical ecology, including intentional or unintentional communication among or between prey species, their predators, and their predators' predators. Such studies are in their infancy in seaweed chemical ecology and represent important areas for future studies. Likewise, we are just starting to learn about seaweed defenses against pathogens and biofoulers in ecologically relevant contexts. Doing the necessary experiments in an ecologically relevant manner is difficult, but many more such studies are needed to advance the field. Important work is ongoing in all areas touched on in this short review. In each there is much more to be learned and many important questions yet to be asked.

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Chapter 10
Bacterial Communities on Macroalgae

Michael W. Friedrich

10.1 Introduction

Macroalgae are important primary producers in the marine environment, alter the ecosystem by influencing sediment structure and water flow, and provide a habitat for many marine organisms. The surface of macroalgae is an important habitat for microorganisms, and healthy macroalgae are consistently colonized by microbial communities (Bolinches et al. 1988; Jensen et al. 1996). Interactions of epiphytic microorganisms with its algal host range from beneficial (Goecke et al. 2010; Wahl 2008) to disease and decomposition (Largo et al. 1995, 1997, 1999; Vairappan et al. 2001; Wang et al. 2008). Algae-associated bacteria have been shown to enhance algal growth and provide nutrients (Croft et al. 2005, 2006; Keshtacherliebson et al. 1995; Goecke et al. 2010), influence release and settlement of algal spores (Joint et al. 2002, 2007; Weinberger et al. 2007; see also Chap. 9 by Amsler and Chap. 11 by Potin), and either enhance or deter the settlement of invertebrate larvae (Dobretsov and Qian 2002; Huggett et al. 2008; Patel et al. 2003; Steinberg and de Nys 2002). Specific bacteria play an important role in the development of normal morphology in several green algae (Marshall et al. 2006; Matsuo et al. 2003; Nakanishi et al. 1996; Provasoli and Pintner 1980). Moreover, algal-associated bacteria produce toxins, signaling compounds, and secondary metabolites, which represent an interesting reservoir for the discovery of bioactive compounds (Egan et al. 2008). Such intriguing microbial interactions are based on cultured bacteria.

The analysis of microbial communities associated with macroalgae, however, is still in its infancy. Recent comprehensive reviews have examined the body of literature available on microbial communities associated with macroalgae, which is, however, largely built on cultivation-based studies (Goecke et al. 2010;

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Olson and Kellogg 2010) with known limitations in adequately describing the composition of natural microbial communities. This chapter focuses on studies analyzing the composition of bacterial communities using molecular biology approaches by sequence information, thereby allowing to identify individual community members based on phylogenetic and functional traits.

10.2 Microbial Communities Associated with Macroalgae

The past two decades have seen tremendous efforts to unravel the diversity of microorganisms in the marine environment (Pernthaler and Amann 2005; Rappe and Giovannoni 2003). Among sessile eukaryotes with microbial colonization, sponges and corals have received the greatest interest, whereas comparatively few studies have analyzed the microbial diversity associated with the surface of macroalgae (Egan et al. 2008), and specifically macroalgae thriving at mesophotic depths are understudied (Olson and Kellogg 2010). Apart from microorganisms of the domain bacteria (see below), protists as well as fungi occur on macroalgae, including a number of pathogenic fungal species (Armstrong et al. 2000; Correa 1997; Raghukumar et al. 1992), but nothing is known about Archaea (Olson and Kellogg 2010).

Traditionally, classification of microorganisms has relied on cultivation, which requires pure cultures for testing physiological, biochemical, and cell biological properties, and suitable media for their growth. Only a small fraction of microorganisms grow on standard media, in some environments this has been estimated to be as low as 0.001–<1%, e.g., in seawater (Amann et al. 1995; Eilers et al. 2000; Fuhrman and Campbell 1998); thus, cultivation of microorganisms may not reflect numerically abundant microbial populations in the habitat they were retrieved from. Until recently, cultivation-based approaches have nevertheless contributed most of our knowledge regarding microorganisms associated with the surface of macroalgae (Goecke et al. 2010). Microscopy and cultivation-based techniques have revealed densities of 10^4–10^7 cells g^{-1} (wet weight) of algal biomass for healthy individuals (Largo et al. 1997; Lewis et al. 1985; Weinberger et al. 1994). Most common isolates retrieved from algal surfaces comprise the genera *Flavobacterium*, *Bacillus*, *Vibrio*, *Pseudomonas*, and *Moraxella* (Bolinches et al. 1988; Chan and Mcmanus 1969; Egan et al. 2008; Lewis et al. 1985). A large number of novel bacteria have been isolated from diverse macroalgal species over the last decade and a number of novel genera especially in the family Flavobacteriaceae have been described (Goecke et al. 2010).

Given the inherent limitations of cultivation-based approaches, cultivation-independent molecular biology approaches are nowadays used to assess the structure of a microbial community (i.e., its diversity and abundance of microbial populations) (Liesack et al. 1997). Cultivation-independent molecular approaches for community study rely on the concept to clone and sequence genes (e.g., the 16S rRNA gene is predominantly used) directly from biomass rather from cultures

(Pace et al. 1986). The molecular tool box is complemented by whole-cell in situ hybridization with rRNA-targeted fluorescently labeled oligonucleotide probes (fluorescent in situ hybridization, FISH) for PCR-independent identification and enumeration (Amann et al. 1995), as well as various PCR-based fingerprinting methods (e.g., DGGE, denaturing gradient gel electrophoresis; T-RFLP, terminal restriction fragment length polymorphism analysis) (Liu et al. 1997; Muyzer et al. 1993). Essentially, sequence-based analysis (i.e., cloning/sequencing) allows to characterize a microbial community at the level of individual phylotypes; however, this approach has been limited in the past by considering insufficient numbers of sequences (and replicate samples) causing under-sampling bias (Green and Bohannan 2006; Hughes et al. 2001). Fingerprinting methods reflect the diversity of the whole PCR amplicon pool, and thus, are powerful tools to compare larger numbers of sample; however, they have limited phylogenetic resolution (Marsh 2005). Therefore, this review focuses mainly on studies that characterized the composition of microbial communities associated with macroalgae using sequence information (Table 10.1).

A number of cultivation studies complemented with molecular cultivation-independent analysis found only little overlap between the identity of isolates and predominant sequences retrieved from the algal host (Bengtsson et al. 2010; Tujula et al. 2010). For example, the strains of the γ-proteobacterial genus *Pseudoalteromonas* have been frequently isolated from Ulvacean algal hosts (Dobretsov and Qian 2002; Egan et al. 2000, 2001; Patel et al. 2003), but were not detected by catalytically amplified reporter deposition (CARD)-FISH on samples of *Ulva australis* (Tujula et al. 2010).

Sequence-based microbial community composition studies (Table 10.1) included a range of macroalgal species representing Rhodophyta ($n = 5$), Phaeophyceae ($n = 4$), Chlorophyta ($n = 6$), and two functionally defined algae from a coral reef, crustose calcifying algae, and turf algae. The majority of studies analyzed up to 300 sequences by conventional Sanger sequencing of clones or DGGE bands, one study analyzed ~900 clones per individual (*Ulva australis*) (Burke et al. 2011b), and one study used pyrosequencing with up to 60,000 sequences from one individual sample (Barott et al. 2011). High-throughput sequencing methods, such as 16S rRNA gene tag pyrosequencing (Sogin et al. 2006), facilitate to retrieve several thousands (to hundreds of thousands) short sequences (100–400 bp).

Among the microbial phyla encountered sequences representing α-Proteobacteria were most numerous across all studies and macroalgal species (Table 10.1). Frequently detected were also bacteria associated with the phyla Bacteroidetes, Planctomycetes, Verrucomicrobia, Cyanobacteria, and δ-Proteobacteria, and on a few algal species Actinobacteria, Chloroflexi, and Firmicutes. Up to 22 different phyla were encountered in a pyrosequencing-based diversity study of four different algae from a coral reef ecosystem (Barott et al. 2011), indicating the high diversity of microbial communities on macroalgae. Planctomycetal sequences were detected on a relatively large number of algae (Table. 10.1), albeit mismatches of the canonical 27F-primer used to most planctomycetal 16S rRNA genes typically result in underrepresentation of Planctomycetes in clone libraries; when using a specific FISH probe,

Table 10.1 16S rRNA gene sequence-based community composition of microorganisms associated with macroalgae

Taxonomic algal group	Algal species (sampling location)	Major bacterial phyla encountered	Representative species	Number of clones/ sequences analyzed	Methods	Experimental details	References
Rhodophyta (Red algae)	*Delisea pulchra* (Bare Island, Botany Bay, Sydney, Australia)	α-, δ- and γ-Proteobacteria, Planctomycetes, Bacteroidetes	n.d.	236/62	CL-RFLP DGGE Direct tissue lysis	Comparison of three host species (sponge, red, and green macroalgae)	Longford et al. (2007)
	Ahnfeltiopsis flabelliformis *Caulacanthus ustulatus*	Cyanobacterium *Acaryochloris* spp.	n.d	–/23	DGGE Bandseq SP Direct tissue lysis	Tracing cyanobacteria on macroalgal surfaces	Ohkubo et al. (2006)
	Porphyra yezoensis (cultivated in the lab)	γ-Proteobacteria, β-Proteobacteria, Bacteroidetes	*Alteromonas* spp.	100/100	CL Direct tissue lysis	Development of a primer for excluding eukaryal templates	Namba et al. (2010)
	Gracilaria vermiculophylla (Kiel fjord, North Sea)	α-Proteobacteria (31–71%) Bacteroidetes (9–41%) Actinobacteria (3–11%) δ-Proteobacteria (~10%) Planctomycetes (~3%)	*Mesorhizobium* spp. (~25%)	60/60^a	DGGE CL, Cotton swab samples	Comparison of three algae and seawater; summer and winter samples	Lachnit et al. (2011)
Phaeophyta (Brown algae)	*Laminaria saccharina* (Kiel, Baltic Sea; Helgoland, North Sea)	α-Proteobacteria (9 phylotypes), γ-Proteobacteria (6) Bacteroidetes (4)	Erythrobacter spp. Roseobacter spp.	170^b 112^b	DGGE CL	Specific microbial populations associated with different parts of the alga, some overlap with bacteria in seawater found	Staufenberger et al. (2008)
	Laminaria hyperborea (Bergen, Norway)	Planctomycetes	RB1 lineage (73–98%)	260	CU SP CL (FISH) scraped biofilm	Over 50% of epiphytic microbial cells (DAPI) were Planctomycetes, seasonal variability	Bengtsson and Ovreas (2010)
	Laminaria hyperborea (Bergen, Norway)	Planctomycetes (47%) α-Proteobacteria (21%) Verrucomicrobia (18%) Cyanobacteria (5%) Bacteroidetes (4%) γ-Proteobacteria (4%)	n.d.	273 bands	DGGE Bdseq, scraped biofilm	Seasonal variation of microbial communities and comparison with seawater	Bengtsson et al. (2010)
	Laminaria hyperborea	α-Proteobacteria	Roseobacter spp.			Follow-up study, proves that cultivation could not retrieve the most relevant bacteria from the natural biofilm	Bengtsson et al. (2011)

	Fucus vesiculosus (Kiel fjord, Germany)	γ-Proteobacteria (22–33%) Bacteroidetes (20–30%) Verrucomicrobia (6–31%) α-Proteobacteria (13–31%) Planctomycetes (3–19%) Cyanobacteria (2–17%)	*Octadecabacter arcticus* (Rhodobacterales) ~20%	$60/60^{a}$	DGGE, CL Cotton swab samples	Comparison of three algae and seawater, summer and winter samples	Lachnit et al. (2011)
	Dictyota bartayresiana (coral reef, Curacao, Netherlands Antilles)	Unknown bacteria (24–38%) Cyanobacteria (18–33%) Proteobacteria (31–34%) Bacteroidetes (10%)	Various unclassified bacteria cyanobacteria	9,500, 16,300	PYR, Direct tissue lysis	Comparison of four algae and reef-building coral spp.	Barott et al. (2011)
Chlorophyta (Green algae)	*Caulerpa taxifolia*	α-Proteobacteria Bacteroidetes δ-Proteobacteria β-Proteobacteria	*Ruegeria* (Rhodobacter group)	$50^{d}/54$	RFLP CL Direct tissue lysis	Geographical different *Caulerpa* specimen were compared from Mediterranean, Tahiti, the Philippines and Australia	Meusnier et al. (2001)
	Ulva compressa *Ulva intestinalis* (Chañaral Bay, Northern Chile)	Bacteroidetes (49%) α-Proteobacteria (15%) Verrucomicrobia (5%) γ-Proteobacteria (9%)	n.d.	79	TRFLP CL Sonication	Three algae and seawater compared, seasonal effects, copper pollution	Hengst et al. (2010)
	Ulva australis (Bare Island, Botany Bay, Sydney, Australia)	α-, δ- and γ-Proteobacteria Planctomycetes Bacteroidetes	n.d.	197/25	CL-RFLP DGGE Direct tissue lysis	Comparison of three host species (sponge, red and green macroalgae)	Longford et al. (2007)
	Ulva australis (Shark Point, Clovelly, NSW, Australia)	α-Proteobacteria (70%) Bacteroidetes (13%)	*Roseobacter* clade (47%)	34/28	DGGE Bdseq cFISH Direct tissue lysis	Diversity and seasonal dynamics, spatial distribution	Tujula et al. (2010)
	Ulva australis (Bare Island, La Perouse and Shark Point, Clovelly, NSW, Australia	α-Proteobacteria (54%) Bacteroidetes (28%) γ-Proteobacteria (8%) Planctomycetes (3%)	Unclassified Rhodobacteraceae (22%)	5293^{e}	CL Microbial cells released from algal surface	Taxonomic in-depth analysis, comparison to seawater community	Burke et al. (2011a, b)
	Ulva prolifera (Jiaozhou Bay, Qingdao)	γ-Proteobacteria (23–53%) α-Proteobacteria (28–35%) CFB group (27%)	Alteromonadales/ Glaciecola	192	DGGE CL cells released by shaking	Comparison of thallus-surface bacterial community composition and surrounding seawater of algal bloom region; two time points	Liu et al. (2011)
	Ulva intestinalis (Kiel fjord, Germany)	α-Proteobacteria (41–71%) Bacteroidetes (5–29%) γ-Proteobacteria (7–15%) OD1-ODP11-WS6-TM7 (5–13%)	*Phyllobacterium* (~14%) (Rhizobiales)	$60/60^{a}$	DGGE CL Cotton swab samples	Comparison of three algae and seawater, summer and winter samples	Lachnit et al. (2011)

(continued)

Table 10.1 (continued)

Taxonomic algal group	Algal species (sampling location)	Major bacterial phyla encountered	Representative species	Number of clones/ sequences analyzed	Methods	Experimental details	References
	Halimeda opuntia (coral reef, Curacao, Netherlands Antilles)	Proteobacteria (31–34%) Cyanobacteria (27%) Unknown bacteria (10–12%) Bacteroidetes (15%) Firmicutes (6–8%)	*Cyanobacteria* Group I (8%)	52,100, 44,800[c]	PYR Direct tissue lysis	Comparison of four algae and reef-building coral spp.	Barott et al. (2011)
Functional groups							
	Turf algae (coral reef, Curacao, Netherlands Antilles)	Proteobacteria (49–57%) Unknown bacteria (10%) Cyanobacteria (5–11%) Firmicutes (8–9%) Bacteroidetes (5–13%) Actinobacteria (2–3%)	*Acidovorax* spp. (11%)	34,000 61,000[c]	PYR Direct tissue lysis	Comparison of four algae and reef–building coral spp.	Barott et al. (2011)
	Crustose coralline algae (coral reef, Curacao, Netherlands Antilles)	Proteobacteria (27–32%) Unknown bacteria (25%) Cyanobacteria (12–20%) Firmicutes (10–18%) Bacteroidetes (15%) Chloroflexi (7%)	*Unclassified Bacteria* (11%)	39,600 36,600[c]	PYR Direct tissue lysis	Comparison of four algae and reef-building coral spp.	Barott et al. (2011)

TRFLP, terminal restriction fragment polymorphism analysis; *DGGE*, denaturing gradient gel electrophoresis; *CU*, culturing; *CL*, clone libraries; *CL-RFLP*, representative clones sequenced after restriction fragment length typing of clones; *Bdseq*, DGGE band sequencing; *SP*, specific primers; *cFISH*, catalyzed reporter deposition fluorescence hybridization; PYR, pyrosequencing; n.d., not determined

[a] ~60 Sequences per alga and season analyzed, DNA pooled from three individuals

[b] Clones ($n = 170$) were from the Baltic Sea algal sample, and 112 clones were from the North Sea algal sample; however, a large number of sequences was from chloroplast 16S rRNA genes ($n = 228$)

[c] Each algal species was analyzed from two different coral sites

[d] ~50 clones per host analyzed by RFLP

[e] Clones from six libraries representing six different *Ulva australis* samples; in addition, ten different seawater samples were analyzed

Bengtsson and Ovreas (2010) could show that Planctomycetes dominate in biofilms on *Laminaria hyperborea* (up to 50% of all DAPI counts), and clone libraries generated with a Planctomycete specific primer set revealed a high diversity of this phylum. Thus, Planctomycetes might be underrepresented in clone libraries of microbial communities of macroalgae studied so far. Whereas similar bacterial phyla are frequently encountered (Table 10.1), algae specific populations, i.e., highly similar (>97%) or identical in sequence could not be identified across all algal taxa examined so far. Nevertheless, 16S rRNA gene sequences of the α-proteobacterial Rhodobacterales, Rhizobiales (*Mesorhizobium* spp.), and *Cyanobacterium* spp. were found as most frequent populations on red, brown, and green algal species (Barott et al. 2011; Burke et al. 2011b; Lachnit et al. 2011; Meusnier et al. 2001; Tujula et al. 2010) (Table 10.1).

10.3 Host-Specific Microbial Communities on Macroalgae?

An important open question in alga–microbe interactions is whether these associations are host-specific. A number of studies report that certain microbial populations appear to be unique to the algal host but were absent in clone libraries or DGGE patterns of the surrounding seawater (Bengtsson et al. 2010; Burke et al. 2011b; Lachnit et al. 2011; Liu et al. 2011; Staufenberger et al. 2008), albeit some overlap might exist at high taxonomic levels, i.e., phyla (Longford et al. 2007). The surrounding seawater and sediment are likely sources of microbial recruitment for algal surfaces. However, small microbial populations might be easily overlooked at limited sample size possibly masking the presence of algal colonizers in seawater. For example, a study on the kelp species *Saccharina latissima* (as *Laminaria saccharina*) involved 170 clones from the algal surface but only 31 clones from seawater (Staufenberger et al. 2008); this is especially critical, as the seawater microbial community was more diverse than that of the algal hosts according to DGGE analysis. Nevertheless, the difference in composition between seawater and algae suggests that algae provide at least a niche for a distinct microbiota. In fact, different algal hosts from the same sampling site had highly dissimilar microbial communities, suggesting that each algal host provides a unique niche for microbial colonization (Barott et al. 2011; Lachnit et al. 2011).

A few studies report the existence of a "core" of specific microbial populations on their host algae. For example, on the kelp species *Laminaria hyperborea* a Planctomycete operational taxonomic unit (OTU) was commonly detected (78% of all samples) over all seasons, albeit the OTU was defined relatively coarsely (95% sequence identity; Bengtsson et al. 2010). Among the macroalgae from the Baltic Sea, between 7 and 16% were identified as algal host-specific populations (OTUs defined >99% sequence identity) across seasonal samples but still not all OTUs were consistently present in summer and winter samples (Lachnit et al. 2011). The detection of a core microbial community is further complicated by patterns of different microbial colonization along algal tissues, or might be subject to succession with the age of the individual alga. On young meristems and cauloids of *Saccharina latissima* microbial communities were more similar to each other than aging blade sections of the same individual (Staufenberger et al. 2008), suggesting that tissue age might contribute to microbial community variability. Conversely, no clear differences were found in microbial communities on meristem and lamina of *Laminaria hyperborea* (Bengtsson et al. 2010), indicating that considerable variability exists even between closely related species.

Several lines of evidence suggest that microbe–macroalgae interactions might not be host-specific when 16S rRNA gene phylogeny is the basis for microbial community assessment (Burke et al. 2011b). (1) Microbial communities can vary considerably among individuals of the same algal species. The microbiota on *Ulva australis* individuals from within the same and three different tidal pools, separated by less than 20 m, were found highly variable (up to 40% based on DGGE analysis; Tujula et al. 2010). A large-scale sequencing analysis revealed that less than 20% of sequences (at 97% sequence identity) were shared among six individuals of *Ulva australis* (Burke et al. 2011b). Also, on *Laminaria hyperborea* variability in community composition was detected between sampling locations (Bengtsson et al. 2010). (2) The algal microbiota varies considerably over seasons. Individuals of *Ulva australis* varied as much as 40% in summer (Tujula et al. 2010). Strong seasonal shifts also occurred in the microbiota of *Fucus vesiculosus*, *Gracilaria vermiculophylla*, and *Ulva intestinalis*; however, shifts were consistent at the phylum level and reoccurred in two consecutive years (Lachnit et al. 2011). The considerable variability among individuals of the same species became especially apparent in the study of the green algae *Ulva australis* based on the resolving power of large-scale sequencing (Burke et al. 2011b). It appears that at least in case of *Ulva australis* a core microbiota does not exist and that a large number of microbial populations are capable of colonizing the algal surface (Burke et al. 2011b).

10.4 A Model of Surface Colonization on Macroalgae

The high variability in microbial colonization of algal surfaces observed in a number of studies has resulted in the proposal that a large functional redundancy exists within the colonizing microbiota (Burke et al. 2011b). If true, then phylogenetic aspects, e.g., which microbial populations (or taxa) are present on the alga, would be inferior to the presence (and expression) of specific functions encoded by their genes. A recent metagenomic analysis of the microbiota on *Ulva australis* supports the hypothesis that the algal surface provides a niche for microorganisms carrying specific functional genes rather than belonging to a specific taxonomic group (Burke et al. 2011a). Despite the high taxonomic variability (~only 15–20% similarity between individuals), the functional composition of genes was highly similar (70%) and a core set of functional genes across all members of the microbial community was detected. Core functions detected at higher rate than in the surrounding seawater encompassed genes involved in detection and movement to the host, attachment and biofilm formation, response to the algal host environment, regulatory mechanisms in response to environmental stimuli, defense, and lateral gene transfer. All these functions were regarded as consistent with the ecological role of the *Ulva australis* microbiota (Burke et al. 2011a). Phylogenetic and functional analysis of the metagenome dataset revealed that the core functions are not restricted to a particular taxonomic group, suggesting that different taxa are responsible for the core functions of the microbial community on *Ulva australis*. Based on their results, Burke et al. (2011a, b) proposed a competitive lottery model for community assembly on the surface of *U. australis*. The competitive lottery model, originally proposed for coral reef fish (Sale 1979), integrates functional and random components of community assembly. According to the model, different species but with similar (or identical) functional traits can occupy the same niche in an ecosystem facilitated through the stochastic chance ("lottery") to get to the particular niche space first (Sale 1979). Translated to microbial community structuring, Burke et al. (2011a,b) argue that microbial populations can colonize the surface of an alga provided they have the necessary function in the form of a particular gene (or sets of genes). The assemblage of microbial population might, however, be determined by stochastics ("lottery") rather than controlled by specific host enforced selection mechanisms that would result in a very specific microbiota that is known from other host–microbe systems. Such a model of microbial community structuring implies that genes (or gene clusters) are more important than microbial taxonomic entities ("species"). In microbiology, the species concept is still a matter of debate and especially lateral transfer of genes renders it difficult to define how a microbial species is defined (Rossello-Mora and Amann 2001). Support for functional genes as drivers of community assembly also comes from the observation that the microbiota on *Ulva australis* abundantly harbors genes necessary for lateral gene transfer (Burke et al. 2011a). Analyzing functional genes revealed biological patterns on *Ulva australis* (Burke et al. 2011a) that were not detected by studying 16S rRNA gene-based phylogenetic community composition (Burke et al. 2011b). Similar observations were made in the human microbiome (Turnbaugh et al. 2009). The repercussions of these findings could have far reaching impacts on studies of microbial community ecology eventually shedding light on differences in the ecology of micro- and macroorganisms.

10.5 Conclusions

The molecular microbial ecology of macroalgal hosts is a rather young field with only small datasets available but with large potentials to influence theory building in microbial ecology and host–microbe interactions. Recent, more in-depth molecular sequence analyses have challenged the notion that host-specific microbial taxa colonize macroalgal surfaces. Rather, a model of algal colonization has been proposed in which specific microbial functional genes govern the structuring of microbial communities and not taxonomic affiliations of microbial populations

(Burke et al. 2011a, b). Methodological improvements, here the application of large-scale sequencing approaches and analyses at the level of individual functional and phylogenetic marker genes, have facilitated to gain insight into novel biological patterns. Naturally, the database of microbial communities on algal host species should be broadened to test the proposed functional gene-driven hypothesis of microbial community structuring. Ultimately, identification of important functional traits might also allow unraveling the role of microorganisms in macroalgae–microbe interactions.

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Chapter 11
Intimate Associations Between Epiphytes, Endophytes, and Parasites of Seaweeds

Philippe Potin

11.1 Introduction

Most, but not all, seaweeds studied in natural ecosystems are plagued by epiphytes, endophytes or other eukaryotic parasites that cause no or few apparent disease symptoms. Hence, such intimate associations can range from mutualism through commensalism to parasitism in a continuous manner (Correa 1994). In shallow hard-bottom marine habitats, seaweeds compete for substrate, nutrients, and light (see Chap. 7 by Edwards and Connell). A planktonic bank of seaweed spores and propagules is periodically and widely distributed in the coastal zone that is ready to settle in all appropriate microhabitats (Wahl and Mark 1999; Lotze et al. 2000). In this context, epibiotism (using other organisms as substrates) illustrates competition for space (e.g., Menge 1991; Underwood 2000; Wahl and Mark 1999). Epibiotic associations comprise a substrate organism (basibiont) and one or several attached species (epibionts). This chapter focuses on associations between seaweeds, and therefore it corresponds to associations between algal basiphytes and epiphytes. A wide variety of algae colonizes other algae representing a continuum between epiphytism and endophytism. Such interactions begin with nonrandom patterns of settlement and recruitment (Gonzalez and Goff 1989; Pearson and Evans 1989, 1990) and artificial substrata are often preferred over nearby living surfaces for epiphytes (Wahl and Mark 1999) very likely depending on the previous colonization of these surfaces by specific bacterial biofilms (Goecke et al. 2010, see also Chap. 10 by Friedrich). Therefore, host specificity was considered as an exception in such interactions. However, the presence of epiphytes, endophytes, and eukaryotic parasites in marine macrophytes results from complex interactions

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between hosts and colonizers that were hardly investigated. These interactions have positive effects, such as providing additional ecological niches, food and protective habitat for animals (Pavia et al. 1999; Karez et al. 2000; Viejo and Åberg 2003; Bittick et al. 2010), as well as negative effects, such as competition with the host for light and nutrients (D'Antonio 1985; Cebrian et al. 1999; Honkanen and Jormalainen 2005); increasing drag (D'Antonio 1985; Hemmi et al. 2005); and favoring the attraction of grazers to the host alga (Bernstein and Jung 1979; Wahl and Hay 1995; Wahl et al. 1997). During the last decades, sustained nutrient enrichment from land-based activities resulted in increased biomass of attached epiphytes in many ecosystems (Rönnberg and Bonsdorff 2004; Russell et al. 2005, see also Chap. 21 by Teichberg et al.) and consequences of global warming may also strongly affect these biotic interactions (Eggert et al. 2010). In addition, closed associations between seaweeds are involved in human affairs when they impact the mariculture or the harvesting of wild populations of economically important seaweeds (Friedlander 1992; Critchley et al. 2004; Hurtado et al. 2006; Vairappan 2006; Gachon et al. 2010, see also Chap. 22 by Buchholz et al.) or when opportunistic species foul artificial substrates (Callow and Callow 2011).

This chapter attempts to summarize a part of the literature available on the biology and ecology of such close associations. The particular focus will be on cross-talk mechanisms involved in host specificity, the role of bacterial biofilms in mediating some interactions, as well as the role of host chemical defenses that impact the diversity of associations through allelopathic interactions. In the context of coastal eutrophication and climate change, these subtle relationships between seaweeds and colonizers at the community level and in human affairs, including algal mariculture or the search for environment-friendly antifouling and antimicrobial strategies, will be an important and emerging field of research.

11.2 Ecology and Biology of Close Biotic Interactions of Seaweeds

11.2.1 Epiphytes

Algal epiphytes are ubiquitous and play major ecological functions in coastal benthic communities. Therefore, the available literature on algal epiphytes is abundant but also very diverse with a lack of a comprehensive review. Algal epiphytes have been studied mainly in terms of species diversity and community ecology. However, in comparison with the abundant literature available on seagrasses, considerably less work has concerned the distribution and effects of epiphytic populations on macroalgal hosts (D'Antonio 1985; Rindi and Guiry 2004). The composition of epiphytic assemblages on macrophyte host surfaces displays strong seasonal and spatial variations (Markham 1969; Whittick 1983; Arrontes 1990; Rindi and Guiry 2004; Leonardi et al. 2006). Old or damaged portions of thalli appear more susceptible to epiphyte colonization (Ballantine 1979; Lobban and Baxter 1983; Ducker and Knox 1984; Pearson and Evans 1989, 1990; Arrontes 1990). Patterns of epiphytic assemblages are also strongly dependent on the intensity of grazing by various invertebrates or fishes (Lubchenco and Gaines 1981). The species composition of epiphyte guilds is also conditioned by physical factors, particularly desiccation and wave action (Hayward 1980; Graham and Hanna 1989; Longtin et al. 2009). These factors strongly impact the distribution and stability of suitable substrata and increase selective forces affecting epiphyte growth (Benzing 1987). Despite substantial work on marine epiphytes, their population ecology has received little attention (Harlin 1987; Longtin and Scrosati 2009; Longtin et al. 2009).

Various types of interactions can be established between basiphytes and epiphytes, but only a few studies, based on both wild and laboratory-infected material, report on the contact surface established between epiphytes and their hosts (Rawlence 1972; Rawlence and Taylor 1972; Ducker and Knox 1984; Gonzalez and Goff 1989; Gonzalez et al. 2003; Dawes et al. 2000; Leonardi et al. 2006). The damage caused by an epiphyte to its basiphyte can be highly variable and is mainly influenced by the type of anatomical association and the incidence of the epiphyte (Fletcher 1995). According to Linskens (1963), holo-epiphytes are those attached to the outer layers of the host, whereas amphi-epiphytes are deeply anchored in the tissue of their hosts. Linskens (1963) suggested, however, that the type of anatomical contact is highly variable and determined by the nature of the partners. Epiphytes attach via single cells, filamentous bases, or massive rhizoidal structures. Host–epiphyte interfaces were typed and their relative abundance and temporal variability were monitored to unravel the mechanisms of host recognition and host damage that could explain the loss of crops and the negative effects of epiphytism in *Gracilaria chilensis* farming (Leonardi et al. 2006): Five types of anatomical relationships were detected. *Infection type I* included the epiphytes weakly attached to the surface of the host and not associated with damage of host tissues (i.e., *Hincksia mitchelliae*, *H. granulosa* and *Ectocarpus acutus*). *Infection type II* included those epiphytes strongly attached to the surface of the host but not associated with any host tissue damage (i.e., *Acrochaetium* sp., *Antithamnionella* sp. and *Colpomenia sinuosa*). *Infection type III* included all the epiphytes that penetrated the outer layer of the host wall without damaging its cortical cells (i.e., *Xenococcus* sp. and *Sahlingia subintegra*). *Infection type IV* included epiphytes penetrating deep into the host cell wall, disorganizing the cortical tissue (i.e., *Ulva lactuca* and *Acrosorium corallinarum*). *Infection type V* included epiphytes that penetrated deeply into the cortex, reached the medullary tissue, and caused destruction of the host's cells in the area around the infection (i.e., *Ceramium rubrum* and *Polysiphonia harveyi*). Prevalence varied with time and with infection type, with types II and III reaching up to 80% and 90% of the thalli, respectively. Severity of epiphyte infection was similar to the distribution of infection prevalence, with crustose epiphytes colonizing up to 80% of the host surface.

It was also noted that epiphytes could actually be present on the host in the field, yet in a "dormant" state, and that they later developed to maturity in the richer culture conditions.

Epiphytes are usually defined as organisms that grow on plants, but do not derive nutrients from their hosts (Linskens 1976). However, one of the most extensively studied relationships is the obligate partnership of the red alga *Vertebrata* (*Polysiphonia) lanosa,* which is a hemiparasite of the fucoid brown alga *Ascophyllum nodosum* (Taylor 1957; Turner and Evans 1977; Garbary et al. 1991; Levin and Mathieson 1991). Perhaps, hemiparasitism is an intermediate step between simple epiphytism and parasitism. The rhizoids of *P. lanosa* penetrate the host and obtain some nutrition from *A. nodosum* (Rawlence and Taylor 1972; Turner and Evans 1977). However, the quantity of carbon obtained by *P. lanosa* is minimal (Harlin and Craigie 1975) and *P. lanosa* is pigmented and capable of photosynthesis (Bidwell 1958; Fralick and Mathieson 1975). Field observations suggest that the distribution and abundance of *V. lanosa* are highly dependent upon the occurrence of injured host tissue and/or number of lateral shoots (Lobban and Baxter 1983; Burke 1986; Pearson and Evans 1989, 1990; Longtin et al. 2009). Recent work by Longtin and Scrosati (2009) in *Ascophyllum nodosum* beds has reinvestigated the various factors that affect the settlement of the red alga *V. lanosa* at the surface of *A. nodosum* including competitive interactions with epiphytic filamentous brown algae (*Elachista fucicola* and *Pylaiella littoralis*) (Longtin et al. 2009)

11.2.2 Pigmented Endophytes

Numerous species of pigmented algal endophytes are associated with red, brown, and green seaweeds (Goff 1982; Correa 1996; Bouarab et al. 2001a; Bown et al. 2003; Eggert et al. 2010). They are generally small, filamentous algae that belong to three main lineages of multicellular algae (Chlorophyta, Phaeophyceae, and Rhodophyta) and inhabit mainly the intercellular spaces of their hosts. They appear to be carbon independent of their hosts (Correa et al. 1988; Correa 1990; Eggert et al. 2010). Therefore, endophytism has arisen independently numerous times throughout the diversification of the multicellular algal lineages and has likely been constrained by selective pressure exerted on epiphytes by grazers (Peters 2003; Amsler et al. 2009; Aumack et al. 2011) or by abiotic conditions and environmental gradients leading to differential levels of desiccation in intertidal seaweeds (Longtin et al. 2009). During the last decade, additional information has become available on the taxonomy, prevalence, and ecology of pigmented endophytes in brown, red, and green algae and some culture and molecular studies have revealed the occurrence of cryptic stages of the life cycles of some important seaweeds such as kelps (Garbary et al. 1999a, b; Hubbard et al. 2003) or green algae (Sussmann and DeWreede 2002) growing endophytically in the tissues of various algal hosts. Difficulties in isolating endophytes into pure culture and the lack of a robust taxonomy constrain our ability to develop a full understanding of their ecology and that of their hosts.

11.2.2.1 Endophytes in Red Algae

The occurrence of epi-endophyte algae in the red algal host *Hymenena falklandica* was recently reported as the first epidemiological study conducted in Argentina (Gauna et al. 2010). The green alga *Epicladia heterotricha* revealed a 100% prevalence of occurrence, particularly in the basal region of the host and low (14%), moderate (28%), and high (58%) severity degrees of infection were registered (Gauna et al. 2010). In contrast, the green epiphyte *Pseudendoclonium submarinum* exhibited a lower frequency of occurrence, close to 3%. The experimental infection of *H. falklandica* by *E. heterotricha* demonstrated that *E. heterotricha* initially behaves as epiphytic but with endophytic filaments growing into the cortex of the host during late infection, while *P. submarinum* was found to be exclusively epiphytic.

A reassessment of the taxonomy of such green algal epi/endophytes has been attempted during the recent years using molecular tools. Their assignment to genus and/or species level has been previously done on the basis of their morphology, but their growth inside an algal host and their simple growth forms, with relatively few reliable diagnostic characters, make their taxonomy problematic (Dixon 1963; White and Boney 1969, 1970; Woelkerling 1971; Bown et al. 2003) and strongly impact the epidemiological studies. Positive identification depends on culturing living isolates to reveal valuable taxonomic characters that are not always apparent in field collected or preserved material (Nielsen and McLachlan 1986; Correa and McLachlan 1991). The relationships between isolates belonging to the green algal genus *Acrochaete* and other chlorophyte taxa were better characterized by the analysis of internal transcribed spacer 2 (ITS2) rDNA sequence variability (Bown et al. 2003). These findings indicate that the taxonomy of *Acrochaete* may need major revision and suggest that species-specific oligonucleotide primers could be used as the basis for a polymerase chain reaction (PCR) assay to assess endophyte diversity within populations of *Chondrus* and related host species (Bown et al. 2003).

11.2.2.2 Endophytes in Brown Algae

Endophyte species of kelps were recently reviewed by Eggert et al. (2010). Some of these endophytes cause only minor changes in their hosts such as tissue darkening, whereas others are known to produce either degradative losses or tumoral lesions accompanied by severe thalli deformations (Apt 1988a; Peters and Schaffelke 1996). Epidemiological studies in populations of kelps demonstrated that infections may affect 100% of the host population (Andrews 1977; Lein et al. 1991; Peters and Schaffelke 1996; Ellertsdottir and Peters 1997). Recent work on the biology and ecology of brown algal endophytes has focused on exploring novel interactions between kelps and brown endophytes in the South-East Pacific Ocean and Antarctic regions, respectively. Along the Pacific coasts of South America, *Macrocystis pyrifera* is infected by *Laminariocolax macrocystis* (Burkhardt and Peters 1998), initially described as *Streblonema macrocystis* (Peters 1991). Recent results showed that galls affecting natural populations of *Lessonia nigrescens* were associated with the infection by a filamentous brown algal endophyte of the genus *Laminariocolax* (Thomas et al. 2009).

Similar patterns of few filamentous algae growing subtidally except within the thalli of the larger chemically defended macroalgae were also observed by Peters (2003) in Antarctica. The endophytes were highly palatable to the amphipod *Gondogeneia antarctica*, suggesting that these filamentous endophytes obtain some protection from mesograzers by growing in association with unpalatable macroalgae (Amsler et al. 2009). These data suggest that macroalgae along the western Antarctic Peninsula rely on grazers to control populations of potentially harmful epiphytes. These results strongly suggest that the chemically defended macroalgal flora lives in mutualism with high densities of mesograzers, providing amphipods with shelter from predation while continually being cleaned of potentially harmful endo/epiphytes (Aumack et al. 2011).

11.2.2.3 Endophytes in Green Algae

Reports on the occurrence of algal endophytes in green algae are scarce. The endophytic filamentous green alga *Acrochaete geniculata* was identified as the causative agent of a disease affecting tank-cultivated *Ulva rigida* (Del Campo et al. 1998). This destructive disease is characterized by green spots, initially located at the basis of the thalli that spread through the host and gradually cause perforations of the frond (Del Campo et al. 1998). Advanced stages of infection result in frond wrinkling and severe tissue loss. Infection is transmitted within 2 weeks when healthy and diseased fronds are cocultivated, whereas previous trials to infect the host in the laboratory with actively reproducing suspensions of the endophyte remained unsuccessful (Del Campo et al. 1998).

11.2.2.4 Life History Stages of Seaweeds as Endophytic Filaments in Other Taxa

Kelp Gametophytes in Red Filamentous Algae

Kelp gametophytes have been extensively studied in the laboratory, but are elusive in nature. They have occasionally been found growing on rocks, and wood, and as epiphytes on crustose coralline algae (Parke 1932; Sakai and Funano 1964; Funano 1969; Kaneko 1973; Kain 1979). Artificial substrata placed in nature have also successfully been utilized for settlement of kelp gametophytes (e.g., Reed et al. 1988). More recently, gametophytes have been found growing endophytically in the cell walls of red algae where they become reproductive and produced juvenile sporophytes (Garbary et al. 1999a, b). Initially, 17 red algal species from western North America were observed with endophytic kelp gametophytes. They were most common in filamentous hosts, and hundreds of gametophytes were observed in many individual host thalli. To date, endophytic gametophytes have only been observed either in situ or in vitro in cultures from the Pacific Ocean (Hubbard et al. 2003). On the one hand, it is possible that the endophytic habit is an accident of spore settlement and that it is of little or no adaptive significance. On the other hand, endophytism may represent a facultative strategy of primary importance to gametophyte growth and reproduction, at least in some species or in some environments. The irregular branching pattern and absence of heterotrichous development in the kelp gametophytes are analogous to that found in many endophytic red algae (e.g., in Acrochaetiales, Garbary et al. 1982) or endophytic green algae [e.g., *Acrochaete*, *Endophyton*, *Phaeophila* (Nielsen and McLachlan 1986)]. These common features suggest a morphological convergence in red, brown, and green algae based on the common adaptation for endophytism. The benefits and drawbacks of the endophytic lifestyle for kelp gametophytes remain unresolved. The small morphology and low density of endophytic gametophytes in culture suggests drawbacks. However, both free-living and endophytic gametophytes can be found in nature (e.g., Kain 1979; Garbary et al. 1999a, b), implying that both lifestyles represent adaptations. Symbiosis could provide protection from grazing and sedimentation, or improve access to light. Fine sediments reduce kelp spore attachment and survival (Devinny and Volse 1978) and the understories of kelp stands experience higher levels of sedimentation than adjacent cleared areas (Eckman et al. 1989; Duggins et al. 1990). Anderson et al. (1997) found that juvenile *Ecklonia* were grazed less when they grew on adult holdfasts. Similarly, red algal hosts may inhibit herbivores from accessing the gametophytes, or the host surface may be more resistant than in epilithic gametophytes (Padilla 1985). It is also possible that endophytes have no better chance of surviving than free-living gametophytes, but the increased diversity of life history strategies may increase the overall likelihood of gametophytes surviving. More recently, molecular and microscopy data revealed that gametophytes of *Alaria*, *Macrocystis,* and *Nereocystis* epi/endophytically grow in the older portions of the thallus of *Lessoniopsis littoralis* (Lane and Saunders 2005). However, developing sporophytes were hardly observed in the field attached to *L. littoralis*, suggesting that endophytic habit is an accident of spore settlement and that it is of little or no adaptive significance.

Green Algal Endophytes as Alternate Life History Phases of *Acrosiphonia* Species

Molecular studies have shown the relationship between the unicellular endophytes ("*Codiolum*" and "*Chlorochytrium*") and their alternative life history stages, the gametophytes of *Acrosiphonia coalita* and *A. arcta* (Sussmann et al. 1999). The population dynamics of the endophyte and their common hosts (*Mazzaella splendens* and "*Petrocelis*") has been explored, showing a seasonal pattern of abundance of the endophyte (Sussmann and DeWreede 2002). A puzzling aspect of the relationship is the presence of many endophytes at the time the host plant is disintegrating. A bet-hedging strategy is proposed for this complex life history; not only are there two different phases adapted to different seasonal conditions, but there are two different hosts (a crustose and a bladed host) for the endophytic sporophyte phase (Sussmann and DeWreede 2002).

11.2.3 Eukaryotic Parasites and Pathogens

In addition with the case of hemiparasitism caused by *V. lanosa* in *A. nodosum* (see above), strict parasitic relationships have been well studied in red algae, but remained nearly unexplored from a physiological point of view in fungal or oomycete colonizers of marine macroalgae.

11.2.3.1 Adelphoparasites and Alloparasites of Red Algae

Some of the algal endophytes in fronds of red algae are nonphotosynthetic and are assumed to obtain carbon from their hosts (Goff 1982). The evolution of these red algal parasites is one of the most fascinating aspects of algal associations: It is common among florideophyte red algae, involving about 8–10% of the species, and has a unique type of development in which parasite nuclei are transferred to host cells and "control" host cell development in a kind of hijacking. It was reinvestigated in the recent years using new molecular tools to better decipher phylogenetic relationships between the host and its parasite (Zuccarello et al. 2004; Kurihara et al. 2010), as well as to generate genomics data on the two partners. A recent work reported the sequencing of the mitochondrial genomes of the free-living gracilarioid *Gracilariopsis andersonii* and its closely related parasite *Gracilariophila oryzoides* to characterize the effect of a parasitic lifestyle on the organellar genomes of red algal parasites (Hancock et al. 2010). This latter paper provides a comprehensive review of the biology of aldelphoparasitism that is summarized below.

Red algal parasites are unusual because the vast majority (80%) of them parasitize species with which they share a recent common ancestor. This strategy has earned them the name "adelphoparasites," from the Greek, adelpho, meaning "kin." Intracellular adelphoparasites are hardly observed in nature, morphologically reduced to a miniature, often colorless pustule and, yet, have independently evolved hundreds of times among the florideophyte red algae. Another part of red algal parasites (20%) are known as alloparasites ("allo" meaning other), which also diverged from free-living species, but then have radiated to exploit more distantly related red algal hosts (Goff et al. 1997; Kurihara et al. 2010). Goff et al. (1997) give two possible scenarios for the origin of parasitic red algae. In one, the parasites are ancestrally epiphytic, later becoming endophytic and eventually parasitic. In the second, the parasites derive directly from spores that lose the ability to survive independently of the parent, following the evolution of a carposporophyte after fertilization in the florideophyte. One possibility is that adelphoparasites arose by the second process while alloparasites arose by the first.

These interactions were extensively studied at a cell biology level by the group of Lynda Goff and Annette Coleman since the 1980s (see Hancock et al. 2010), but little is known about how these algal parasites affect their hosts at an organismic level and even less at the population level. Research has concentrated on assessing changes in the host at the cellular level (Kugrens and West 1973; Goff 1976) or in detecting translocation of substances between partners (e.g., Court 1980; Kremer 1983). Kremer (1983) showed that although there was carbon transfer in the form of the photoassimilate digeneaside and of amino acids from the host *Rhodomela confervoides* to its parasite *Harveyella mirabilis*, carbon fixed by the host was enough to cover the needs of both the parasite and the host. There are, though, indications that parasitized hosts are more susceptible to removal from the population following local tissue destruction and a decrease in growing tips (Goff 1976). Few studies have specifically evaluated the effects of algal parasitic infections on the host, and these demonstrated reduced growth rates and elongation of the host thallus (Nonomura 1979; Apt 1984). It was shown that infections by the red alga *Hypneocolax stellaris* reduced the growth rate of its host *Hypnea musciformis* by 40% in the field and up to 70% in laboratory trials (Apt 1984).

In contrast with the excellent knowledge on the life history strategies of red algal parasites, the molecular and genomic consequences of becoming a parasite remained unknown until the recent work by Hancock et al. (2010). It reports the sequencing of the mitochondrial genomes of the free-living *Gracilariopsis andersonii* and its closely related parasite *Gracilariophila oryzoides*. Whereas the parasite genome is similar to the host in many ways, the genes encoding the essential proteins *atp8* and *sdhc* are pseudogenes in the parasite. The mitochondrial genome of a parasite from a different class of red algae, *Plocamiocolax pulvinata*, has also lost the *atp*8 gene entirely, indicating that this gene is no longer critical in red algal parasite mitochondria. The trend toward the loss of *atp8* is significant considering that rapid rates of evolution are not occurring among the majority of mitochondrial genes. This creates a bit of a paradox because genes considered of vital importance are being lost while, at the same time, there are clearly selective forces maintaining the genome sequence from further losses and accelerated mutational rates. Further analysis of host and parasite nuclear DNA may elucidate some fundamental genomic shifts and molecular changes that have resulted in a parasitic existence (Hancock et al. 2010). In addition, it is interesting to mention that the galactans from *Tikvahiella candida*, an adelphoparasite of *Solieria robusta*, closely resemble those of its host and furnish evidence in support of a close phylogenetic relationship between the two species (Chiovitti et al. 1999). Similarly with the importance of cell wall galactans in the host perception by spores of some green algal endophytes (Bouarab et al. 1999) and oomycete spores (Uppalapati et al. 2001), it is tempting to speculate that part of the host specificity in red alga parasitism has evolved through sophisticated surface signal perception. Future work in this field will undoubtedly beneficiate of comparative transcriptome analysis using RNAseq that will reveal the expression and the regulation of both host and parasite genes in parasitized red algae as recently done in algal oomycete interactions (see below).

11.2.3.2 Fungal and Oomycete Parasites and/or Pathogens

Considering the vast lack of knowledge and the importance to seaweed aquaculture, the significance of oomycetes and fungi infecting marine algae was outlined in two recent reviews (Gachon et al. 2010; Li et al. 2010) and in a book chapter (Strittmatter et al. 2009). A comprehensive report (Li et al. 2010) included 15 species of oomycetes, six species of chytrids, 31 Ascomycota species, and one species of mitosporic fungi. In nature, both the oomycetes and chytrids frequently occurred and induced prevalence of disease, which could destroy the populations of host plants greatly. However, the Ascomycota growing on algae have never occurred as epidemics so far. Further investigations are required in this field, such as performing tests to satisfy Koch's postulates, investigations of host specificity, interactions between host and parasite, and the potential effects of environmental factors on occurrence of a disease.

Despite their small size and ephemeral life stages, filamentous brown algae are plagued by various pathogens, including viruses (Müller et al. 1998), which are not commented in this chapter, which focuses on eukaryotic parasites. In addition, numerous historical records described ectocarpoids with abnormal sporangia or vegetative cells suspected to contain unknown parasites (Rattray 1885; Müller et al. 1998). The oomycete *Eurychasma dicksonii* has been described mainly in wild populations of *Pylaiella littoralis* (Küpper and Müller 1999), but it displays a broad host range and infects various brown algae, including *Ectocarpus* (Müller et al. 1999), in which it was initially described by Wright (1879). *E. dicksonii* belongs to the most early branching clade within the oomycete lineage (Sekimoto et al. 2008; Küpper et al. 2006).

11.3 Cross-Talk Between Host and Colonizers and Defenses Against Colonization

Resistance against epibionts can be generally mediated by either structural or chemical means, with both mechanisms interfering with the settling and penetration of spores or propagules. Algal basiphytes can exhibit a variety of defenses against attachment and colonization (Ducker and Knox 1984), including rapid growth by having ephemeral life histories (den Hartog 1972), changes in pH at the plant surface, and sloughing of outer cell walls *(Ulva,* coralline algae) (Filion-Myklebust and Norton 1981; Johansen 1981; Moss 1982; Steneck 1982; Russell and Veltcamp 1984). *Chondrus crispus* will shed outer layers of cell wall and cuticule glycoproteins (Craigie et al. 1992), whereas *Ascophyllum* produces slime and may lose an entire epidermal layer. *Eucheuma,* a carrageenophyte, has a slimy surface during growth and is free of epiphytes, but when it ceases growth, the plant surface loses that slime and becomes epiphytized (Dawes et al. 2000). Survivorship of epiphyte recruits may also be related to the host, as epiphytes may be less exposed to herbivore pressure when associated with a chemically defended host (Hay 1986; Amsler et al. 2009) and endophytes may survive by avoiding grazing when embedded in host tissues (Amsler et al. 2009). Allelopathy occurs through the exudation of antifouling compounds such as phenolics by the two species of *Sargassum* in the Sargasso Sea (Sieburth and Conover 1965) or iodinated compounds by species of *Laminaria.*

In comparison with epiphytism, alga-parasite or pathogen interactions are generally highly specific and characterized by typical symptoms (for reviews, see Andrews 1976, 1977; Fujita 1990; Goff 1982; Correa 1996; Eggert et al. 2010). Some of the biochemical bases of the responses of seaweeds toward algal endophyte infection have been uncovered recently with either biochemical emphasis (Potin et al. 2002; Weinberger 2007; Cosse et al. 2008; Potin 2008; Weinberger and Potin 2010) or ecological emphasis (Pohnert 2004; Amsler and Fairhead 2006). This contribution does not aim to add one more review on a specific aspect of this research field but rather provide further understanding of the role of cross-talk mechanisms involved in host specificity as well as host chemical defenses that impact the diversity of associations.

11.3.1 Cross-Talk Involved in Host Colonization

Host specificity by several epiphytic or endophytic algal species is a dramatic example of nonrandom settlement and recruitment (Ducker and Knox 1984). In terrestrial plant–fungus mutualistic or pathogenic associations, surface compounds of the host, such as wax and other cell wall compounds, were shown to provide signals to the pathogen in the early stages of colonization. Cell wall polysaccharides from the host are also a source of settlement cues for successful colonization of red seaweeds by swimming spores of pigmented endophytes. Interestingly, the causative agent of green patch disease in the red alga *Mazzaella laminarioides,* the endophytic green alga *Endophyton ramosum,* colonizes carrageenan-producing red algae (carrageenophyte), whereas agar producers (agarophytes) remain uninfected (Sanchez et al. 1996). Surprisingly, another green algal endophytic pathogen, *Acrochaete operculata,* infects carrageenophytes containing lambda-carrageenan more successfully than carrageenophytes containing kappa-carrageenan. When zoospores of *A. operculata* settle and germinate, the vegetative filaments of the parasite completely invade sporophytic fronds of *C. crispus*, which contain lambda-carrageenan. In contrast, gametophytic fronds—containing kappa-carrageenan—are not infected beyond the epidermis and outer cortex (Correa and McLachlan 1991). Recognition by the pathogen of the carrageenan oligomeric degradation products of the host cell walls governs this interaction (Bouarab et al. 1999). Another example of host recognition through cell wall polysaccharides was also partly elucidated in the case of *Olpidiopsis* (*Pythium) porphyrae*, the oomycete agent of red rot disease in *Porphyra yezoensis*. Porphyran, the sulfated agar that characterized the cell wall of the red algal Bangiales, was shown to enhance zoospore attachment, encystment, and appressorium formation.

Here again, sulfation is likely an important cue in signal recognition because agarose, a neutral agar fraction, did not enhance appressorium formation. However, *O. porphyrae* ultimately only infects *Porphyra yezoensis* and *Bangia atropurpurea* and protoplast fusion of *P. yezoensis* with the resistant *Porphyra tenuipedalis* resulted in hybrids with reduced susceptibility. Therefore, probably other signals are involved to increase specificity leading to selective infection.

Various oomycetes are able to infect other red algae, but the spectrum of compatible hosts is usually narrow (West et al. 2006). For example, a strain of *Olpidiopsis* sp. from Madagascar that had been isolated from *Bostrychia moritziana* was also able to infect certain isolates of *B. tenella*, *B. radicans,* and *B. radicosa*, but no other species (West et al. 2006). Five other species of *Bostrychia* were ultimately resistant, as were six different species of *Stictosiphonia*, *Lophosiphonia*, *Neosiphonia,* and *Polysiphonia*. Interestingly, *Bostrychia* isolates originating from Madagascar were in most cases susceptible, and strains from other parts of the world mostly resistant, which seemingly indicates the existence of pathovars (strains of the same species with distinctive pathogenicity due to coevolution with different hosts) among algal pathogens.

Surprisingly, basal oomycetes, such as *Eurychasma dicksonii*, which is the most common and widespread eukaryotic pathogen of marine algae (Gachon et al. 2009), appear far less specific than *O. porphyrae*. It occurs in all cold and temperate seas worldwide (Sekimoto et al. 2008). In culture, it infects virtually all species of brown algae tested (more than 40, Müller et al. 1999), including representatives of all major orders of this phylum. qPCR and microscopic observations made on laboratory-controlled cultures revealed that clonal brown algal strains exhibit different levels of resistance against *Eurychasma*, ranging from high susceptibility to complete absence of symptoms (Gachon et al. 2009). In the coevolution race between parasites and hosts, the parasites quickly overcome new resistance strategies by the host. This process should lead to local adaptation, where a parasite population has a higher mean performance on local (sympatric) versus foreign (allopatric) host populations. Hence, this latter study opens the perspective of combining large-scale disease monitoring in the field with laboratory-controlled experiments on the genome model seaweed *Ectocarpus siliculosus* to improve our understanding of host specificity in brown algal diseases (Grenville-Briggs et al. 2011).

11.3.2 "Ménages à trois," Quorum Sensing Mediated Bacterial–Macroalgal Interactions Modulate Colonization

In marine environments, the space competitors include, in addition to macrophytes, sedentary animals and the periphytic community of microalgae, cyanobacteria, heterotrophic microbes, and protists (see Chap. 7 by Edwards and Connell). The bacterial communities that are associated with macroalgae often provide further settlement cues for macrofoulers, which has in particular been studied with coralline crustose algae (Wieczorek and Todd 1998; Steinberg and deNys 2002; see also Chap. 10 by Friedrich). Shifts in the community composition of alga-associated bacterial communities may potentially result in changed availability of such cues and subsequently in changed intensity of fouling (Steinberg and deNys 2002).

Two recent reports show that the main determinant of the composition and structure of epiphytic bacterial communities at the surfaces of various seaweeds is the nature of the algal host (Hengst et al. 2010; Lachnit et al. 2011). Algae clearly shape the structure and composition of microbial communities in their vicinity (Lam and Harder 2007; Lam et al. 2007). On the other hand, they are also affected by these microorganisms. Certain bacteria have been shown to provide their host algae with growth factors, nutrients, or protection from settlement by other micro- or macrofoulers (Armstrong et al. 2001; Dobretsov and Qian 2002; Matsuo et al. 2005; Zheng et al. 2005) and nonpalatable epiphytes potentially protect more palatable hosts from grazing (Karez et al. 2000). Quorum sensing (QS) is a cell-to-cell communication mechanism that allows bacteria to coordinate swarming, biofilm formation, stress resistance, and production of secondary metabolites in response to an excess of the threshold of QS signals (Paul and Ritson-Williams 2008; Dobretsov et al. 2009). Gram-negative bacteria, such as *Pseudomonas* or *Vibrio* strains, produce *N*-acyl homoserine lactones (AHLs) as signaling compounds. *Pseudomonas* spp. are also known to produce diketopiperazines acting as QS signals (Dickschat 2010). The signal molecules γ-butyrolactones and oligopeptides are known to be synthesized by Gram-positive bacteria, e.g., members of the genera *Streptomyces* or *Bacillus* (reviewed by Dobretsov et al. 2009). The interaction between zoospores of eukaryotic green macroalgae (Ulvales) with *Vibrio anguillarum* indicates algal susceptibility to quorum sensing AHL molecules (Joint et al. 2002; Wheeler et al. 2006). Although the specific mechanism regulating these responses to AHLs is not known, it was shown that the AHL molecules affect the calcium influx into the spores of *Ulva* sp., affecting their motility toward the surfaces where they eventually settle (Diggle et al. 2007; Joint et al. 2007). In addition, it has been demonstrated that life cycle completion and spore release in the red epiphytic alga *Acrochaetium* sp. strongly depend on AHLs, which are produced by bacteria associated with the basiphyte *Gracilaria chilensis* (Weinberger et al. 2007). These findings of AHL perception in green and red algae confirm that AHL signaling is more widespread among eukaryotes than previously thought. This indicates a more general importance of the associated microbial communities in interactions with macroalgae.

During the past decade it has been shown that various macroalgae are able to stimulate, inhibit, or inactivate QS signals in bacteria by producing QS inhibitors or analogs thereof (Maximilien et al. 1998; Joint et al. 2007; Kanagasabhapathy et al. 2009). The Australian red macroalga *Delisea pulchra* produces halogenated furanones, structural analogs to *N*-acyl homoserine lactones. These furanones protect the algal surfaces by interfering with AHL-regulated processes and selectively inhibit bacterial colonization and biofilm formation (Maximilien et al. 1998; Rasmussen et al. 2000; Manefield et al. 2002). In addition to the furanones of

D. pulchra, a variety of bacteria and eukaryotes have been shown to produce cyclic dipeptides that can act as AHL mimics and affect QS-regulated behavior in other bacteria (Dobretsov et al. 2009; Dickschat 2010). Recently, Kanagasabhapathy et al. (2009) suggested that certain epibiotic bacteria from the brown macroalga *Colpomenia sinuosa* may play a role in defense mechanisms and suppress the settlement of other competitive bacteria by producing quorum sensing inhibitors (QSI) or QSI-like compounds.

11.3.3 Allelopathic Interactions and Induced Defenses

Allelopathy was initially defined when a plant secretes toxic biochemicals, such as phytotoxic root exudates (Bais et al. 2003) into its environment. These toxic compounds, called allelochemicals, can have adverse effects on the growth of other plants that come in contact with them. Allelopathy provides a strong advantage in the competition for space by interfering with settlement and/or expansive growth of competitors. According to Gross (2003), in aquatic environments, allelopathy could be extended to include negative influences between photosynthetic organisms and other organisms as well as antifouling strategies (see also Chap. 9 by Amsler).

One of the most dramatic and recent examples of allelopathy between macroalgae in temperate systems is seen in the introduced Japanese alga *Bonnemaisonia hamifera,* which has become one of the most common red algae in Sweden during the last decades (Svensson et al. 2009). Its life history involves an alternation between morphologically different gametophytes and tetrasporophytes and it seems that only filamentous tetrasporophytes (formerly described as a distinct species *Trailliella*) are propagating, often growing as an epiphyte on native algae, primarily *Corallina officinalis* and *Furcellaria fastigiata*. *B. hamifera* was coated on surfaces to estimate settling success of native algal spores. Some field experiments also tested whether this substance can be transferred among species by placing exotic adjacent to native algae under simulated wave action. These authors showed that at natural concentrations, 4-bromo-heptanone, the most abundant brominated compounds in the alga, inhibits settlement of spores from native algal species. Furthermore, the substance can be transferred from *B. hamifera* to the native species. The mechanism of transferring 4-bromo-heptanone to other surfaces might enable the algae to “reserve” space for future colonization, as native algae cannot settle on the coated surfaces. This promising study is the first to show that invasions by exotic algae are facilitated by allelopathy and that chemical defenses can be transferred from exotic to native species (Svensson et al. 2009; see also Chap. 12 by Andreakis and Schaffelke). It is in agreement with the Novel Weapons Hypothesis that predicts that exotic species will be successful if they possess biochemicals unique to their new range (Callaway and Ridenour 2004). *B. hamifera* is also found to be released from predators in the archipelago of Tjärnö (Enge et al.

2009) and another polybrominated compound 1,1,3,3-tetrabromo-2-heptanone inhibits also bacterial colonization (Nylund et al. 2008).

Other examples of allelopathic interactions have been also recently reviewed by Jormalainen and Honkanen (2008) in bloom-forming macroalgae, such as *Ulva fenestrata*, *Ulvaria,* and *Pylaiella littoralis* that gain competitive success using toxic exudates against germlings of canopy-forming seaweeds (Nelson et al. 2003; Råberg et al. 2005). Recently also, the invasive red alga *Lophocladia lallemandii* was observed growing as an epiphyte on *C. taxifolia*, and levels of caulerpenyne were found to be higher on *C. taxifolia* that was epiphytized by *L. lallemandii* (Box et al. 2008). Additionally, activities of antioxidant enzymes, catalase and superoxide dismutase, and H_2O_2 production were higher in epiphytized *C. taxifolia* than in thalli that were not epiphytized by *L. lallemandii*, pointing as the evolution of a defensive mechanism against the new invasive algal epiphyte using caulerpynyne, previously proposed as an allelopathic substance in the invasion success of *C. taxifolia* (Pohnert 2004).

In crustose coralline algae also, allelopathy may be an important means to prevent overgrowth by canopy-forming macroalgae (reviewed by Gross 2003). The crustose coralline alga, *Lithophyllum* sp., produces an allelopathic, nonpolar substance that destroys zoospores of the brown alga, *Laminaria religiosa* (Suzuki et al. 1998). Suzuki et al. (1998) suggested that the reduction of epiphytes due to allelopathy may contribute to the predominance of crustose coralline algae in the coastal region of the Northern Japan Sea. In another study, extracts from the crustose coralline alga *Lithophyllum yessoense* inhibited spore settlement of 14, and germination of spores of 13, of the total of 17 tested macroalgal species (Kim et al. 2004). Kim et al. (2004) suggested that *L. yessoense* probably has multiple allelochemicals, including water-soluble exudates, to cope with macroalgal recruits. More recently, the algal spore lytic fatty acid hydroperoxide of heptadeca-5,8,11-trienoic acid (HpDTE: C17:3) was isolated from the crustose coralline seaweed *Lithophyllum yessoense*. HpDTE showed more than 50% lysis at a concentration of 5 $\mu g\ mL^{-1}$ against the spores of three chlorophyte species, nine rhodophytes, four phaeophytes, and the cells of four phytoplankton species. Lysis activity increased with the number of double bonds and carbon atoms in the fatty acid derivatives (Luyen et al. 2008).

The wound response of the red alga *G. chilensis* involves the release of free fatty acids as well as the hydroxylated eicosanoids, 8R-hydroxy eicosatetraenoic acid (8-HETE) and 7S,8R-dihydroxy eicosatetraenoic acid (7,8-di-HETE) (Lion et al. 2006). While the release of free arachidonic acid and subsequent formation of 8-HETE is likely controlled by phospholipase A, 7,8-di-HETE production is independent of this lipase. This dihydroxylated fatty acid might be directly released from galactolipids that contained 8-HETE or 7,8-di-HETE (Lion et al. 2006). In this context, the induced chemical defense response of the red alga *G. chilensis* against epiphytes was also investigated. An extract of an epiphyte challenged alga was shown to trigger a defense response (Weinberger et al. 2011). The hormonally active metabolite(s) could further be purified by reverse phase RP-HPLC. Treatment with the extract or the fraction resulted in pronounced changes of the chemical profile of the alga and in an increased resistance against spores of the epiphytic red alga *Acrochaetium* sp. Semiquantitative RT-PCR and enzyme assays demonstrated that this metabolic response occurs in succession of an upregulation of lipoxygenases and phospholipase A2 activity. Even if this strongly suggests the involvement of regulatory oxylipins, the known plant hormone jasmonic acid and the algal metabolite prostaglandin E2 do not trigger comparable defense responses.

Interestingly also, *C. crispus* gametophytes synthesize ultraviolet absorbing compounds around the sites of penetration of zoospores of the green endophyte *A. operculata*, whereas this response is absent in the sensitive generation (Bouarab et al. 2004). These findings are reminiscent of the deposition of phenolic compounds in higher plant–fungus or oomycete interactions (McLusky et al. 1999). Although the exact structure of these ultraviolet absorbing compounds remains to be elucidated, their aromatic nature suggests that the perception of the pathogen induces a pathway related to the phenylpropanoid metabolism of terrestrial plants. Indeed, *A. operculata* extracts activated two key enzymes of this pathway, shikimate dehydrogenase and phenylalanine ammonia-lyase (Bouarab et al. 2004) that are also activated by oxylipins.

The only very clear case of nonphlorotannin brown algal secondary metabolites acting as antifoulants in nature that we are aware of is in *Dictyota menstrualis* (Order Dictyotales). Schmitt et al. (1995) reported that *D. menstrualis* was noticeably less fouled in nature than other macroalgae and that bryozoan larvae would not settle on *D. menstrualis* in laboratory bioassays even though they would contact its surface and would settle on several other species of brown and red macroalgae.

Extracts of *Lobophora variegata* (Order Dictyotales) from the Bahamas have particularly strong antifungal bioactivity and Lane et al. (2009) identified the cyclic lactone, lobophorolide, as a defensive compound with significant bioactivity at exceptionally low concentrations against both pathogenic and saprophytic sympatric fungi. Although *L. variegata* from 46 of 51 samples collected at ten sites in the Bahamas contained measurable, bioactive concentrations of lobophorolide, it was not present in two collections from the Red Sea even though crude extracts of the Red Sea algae did have antifungal bioactivity. This indicates that although *L. variegata* from different regions may be chemically defended against pathogens, the same specific compounds may not be involved.

Although the vast majority of the investigations into the defensive chemical ecology of macroalgae have focused on roles of secondary metabolites (see Chap. 9 by Amsler), recent work has demonstrated that both red and brown algae employ oxidative burst defenses against pathogens, a defensive mechanism that has been recognized in terrestrial plants for a number of years (reviewed by Lamb and Dixon 1997; Wojtaszek 1997; Mahalingam and Fedoroff 2003; see also Chap. 6 by Bischof and Rautenberger).

This was first discovered in red algae, where cell wall degradation products elicit a rapid release of H_2O_2 that is toxic to epiphytic bacteria (Weinberger et al. 1999, 2001; Weinberger and Friedlander 2000). Küpper et al. (2001) demonstrated an analogous response in *Laminaria digitata* (Order Laminariales), which produces a rapid oxidative burst of H_2O_2 and O_2—in response to oligomeric degradation products of alginate (a major cell wall component of *L. digitata* and other brown algae). Küpper et al. (2001) also reported that H_2O_2 concentrations in the range released by the algae were toxic to pathogenic, alginate-degrading bacteria and, using histological techniques, demonstrated that the response was primarily confined to the meristoderm. These authors also began to dissect the underlying physiological mechanisms and showed that at least some of the mechanisms are likely conserved within the oxidative burst responses of algae, terrestrial plants, and animals. Küpper et al. (2002) surveyed 45 species of brown algae from 11 Orders for constitutive vs. induced production of H_2O_2. They reported that oxidative bursts in response to alginate oligomers were common in sporophytes in the Laminariales and Desmarestiales but not in their filamentous gametophyte stages. One species (*Pylaiella littoralis*) from the Ectocarpales had an oxidative burst response but ten other ectocarpalean species did not. Members of the Fucales had high constitutive production of H_2O_2 but most did not produce additional H_2O_2 in response to alginate oligomers. Küpper et al. (2002) also reported that axenic sporophytes of *Macrocystis pyrifera* (Order Laminariales) were rapidly infected by pathogenic bacteria when the oxidative burst response was blocked with an NAD(P)H oxidase inhibitor but not in controls, and that when nonaxenic *M. pyrifera* or *L. digitata* sporophytes were treated with the inhibitor, they were rapidly attacked by their natural bacterial flora. These authors also demonstrated that the oxidative burst response is important in resistance of both *M. pyrifera* and *L. digitata* to the pathogenic brown algal endophytes, *Laminariocolax tomentosoides* and *Laminariocolax macrocystis*, although the response took 7 days to occur and likely involves elicitation of other structural or chemical defenses (Küpper et al. 2002).

11.4 Impacts of Close Associations

11.4.1 Community Context

The consequences of epibiotism and endobiosis for the host algae are not necessarily negative, but instead depend on the community context as discussed recently in Jormalainen and Honkanen (2008). Examples of positive effects of epibiont removal by grazers are numerous and depend strongly of the type of interactions established among hosts, epibiota, and grazers. In many cases grazers, often gastropods, can drastically counteract the negative influences of epibiotism.

Epibiota on the host alga may modify the host's susceptibility to herbivores such that it would decrease or increase susceptibility to herbivores. Wahl and Hay (1995) took the host species as the reference point, and classified epibiosis-caused decreases in herbivory as "associational resistance" and epibiosis-caused increases in herbivory as "shared doom." The same phenomena have also been called "protective coating" and "co-consumption," respectively (Karez et al. 2000). Both these epibiosis-related modifications of susceptibility to herbivory have been found in macroalgae (critically reviewed by Jormalainen and Honkanen 2008).

The community context where macroalgae are susceptible to multiple natural enemies, including herbivores and epibionts, and where the susceptibility to one enemy may depend on the occurrence of others, implies that the patterns of natural selection for resistance to epibiotism and resistance to herbivory may be correlated. When enemies tend to coexist on the same hosts, generalized defenses, i.e., traits that provide resistance to assorted enemies, are expected to evolve (Rausher 1996). There are some data supporting such multiple functions of macroalgal secondary metabolites*:* The diterpene alcohols pachydictyol A and dictyol E from *Dictyota menstrualis*, which provide resistance to herbivores (reviewed in Hay and Steinberg 1992), also prevent fouling organisms from colonizing the surface (Schmitt et al. 1995). Similarly, brown algal phlorotannins have been suggested to have multiple functions, e.g., to act both against herbivores and epibiota (reviewed in Amsler and Fairhead 2006). This is also the case of some oxylipins, which are allelopathic substances and were also shown to deter herbivores (Hay et al. 1998).

Epibiosis and grazing are very likely to be intimately interdependent in the influence of both community dynamics and the evolution of resistance traits.

11.4.2 Implications to Seaweed Mariculture

Epiphytes, endophytes, and parasites are well involved in human affairs, as when they increase the cost for mariculture of economically important seaweeds (Friedlander 1992; see also Chap. 22 by Buchholz et al.). Epiphytism has been considered one significant problem in seaweed cultivation (Fletcher 1995; Oliveira et al. 2000; Ask and Azanza 2002; Lüning and Pang 2003). Massive monocultures of algae offer ideal conditions for the growth of epiphytes and propagation of diseases (Wheeler et al. 1981; Fletcher 1995; Lüning and Pang 2003). Epiphytes also produce a series of undesired effects in the production of the host depending on the extent of the contamination (Fletcher 1995). Some important problems with epiphytes have been attributed to (1) competition for nutrients (Buschmann and Gómez 1993), (2) shading (Fletcher 1995), (3) increased weight and drag (Kuschel and Buschmann 1991; Buschmann and Gómez 1993), (4) the possible liberation by the epiphyte of growth inhibiting compounds that affect the host (Santelices and Varela 1993), and (5) a decrease in the reproductive output of the infected host (D'Antonio 1985).

Methods for controlling epiphytes have been described and utilized in cultures of *Gracilaria* (cf. Fletcher 1995). However, many of these methods can only be used in cultivation tanks and are more difficult to apply to open ocean cultivation.

The concern in seaweed mariculture with epiphytism has led to special attention being directed to the selection of resistant strains and to knowledge of the strategies developed by the host to avoid epiphytism (e.g., Santelices and Ugarte 1990; Santelices 1992; Fletcher 1995; Ask and Azanza 2002). For example, the ability to produce compounds, which deter the settlement and growth of epiphytic organisms, has been described in some algae of commercial value (Santelices

1992; Jennings and Steinberg 1997; Harder et al. 2004; Hellio et al. 2004). On the other hand, it has been demonstrated that the capacity to resist an attack depends on the host susceptibility to epiphytes. As mentioned earlier, the presence of different types of carrageenan in the different reproductive phases of *Chondrus crispus* confers a differential adaptation in recognizing an attack by endophytic organisms (Bouarab et al. 1999, 2001b).

Farming of red algal eucheumoids in South-East Asia has been threatened recently by the occurrence of various diseases, mainly "ice-ice", during which parts of the plant turn white from primary or secondary attacks by bacteria and fungi, as well as heavy colonization by endo/epiphytic filamentous red algae (EFAs) of the *Polysiphonia* type, which results in swelling of the host tissue followed by fragmentation and rotting (Critchley et al. 2004). In successive outbreaks of epiphyte infestation, in the Calaguas Islands, the impact of the disease was economically, socially, and environmentally very serious as the farmers became disillusioned and they either moved to other cultivation sites (thus further propagating the epidemy) or returned to the environmentally damaging practices of dynamite or cyanide reef fishing. Production thus declined markedly in this region, from 6,000T per year during 1997–1999 to nil in 2001. At the levels of the Philippines production *Kappaphycus alvarezii* ("Cottonii") farms also are sensitive to smothering by other pest weeds, such as the green algae *Ulva* and *Chaetomorpha* and the brown alga *Hydroclathrus*, as well as to grazing by siganidae herbivory fishes (e.g., rabbit fish) and to marked fluctuations in water temperature due to warm water events. Farmers now tend to grow Cottonii for 45 days (or less) instead of 60 days, resulting in a lower quality of the harvest in terms of biomass and colloid content. The productivity of some *Kappaphycus* farms is decreasing and one estimate indicates that the losses due to diseases now represent about 15% of the potential crop of the Philippines and Indonesia, with a conservative estimated value of US$ 5–10 million to the farmers. That this does not show up yet in the production figures is due to the extension of production areas (i.e., increased hectarage of farming activities, but there is a marked decline in productivity per unit area in certain farms). If the situation is not addressed there is a very real risk that the raw material source in many areas of production could be compromised if a particularly virulent epiphyte/pathogen strain were to arise. In Malaysia also, cultured seaweed became susceptible to epiphytes in the dry seasons between March–June and September–November. Findings revealed *Neosiphonia savatieri* as the dominant infecting epiphyte, representing up to 80–85% of the epiphytes present during peak seasons. Besides *N. savatieri*, *Neosiphonia apiculata*, *Ceramium* sp., *Acanthophora* sp., and *Centroceras* sp. were observed in smaller quantities (Vairappan 2006; Vairappan et al. 2008).

Similarly, there is general agreement that epiphytism is one of the major biological problems in *Gracilaria* farms (Pringle et al. 1989, reviewed by Fletcher 1995) due to the high density of individuals essentially maintained under monoculture conditions. These conditions are known to make the host more susceptible to pests in general and to epiphytes in particular (Friedlander 1992). Competition between hosts and their epiphytes has been demonstrated under natural and artificial conditions of growth (Arrontes 1990; Friedlander and Ben-Amotz 1991;

Svirski et al. 1993), and the extent of the damage is clearly determined by the intensity of the infections (Cancino et al. 1987; Buschmann and Gomez 1993). Farming of *Gracilaria chilensis* during the last 40 years is a clear example of how detrimental epiphytes may become (Kuschel and Buschmann 1991; Pizarro and Santelices 1993).

In addition, negative effects on the economic value of brown and red algae infested by endophytes have been reported (Yoshida and Akiyama 1979; Apt 1988a, b). The endophytic phaeophycean *Laminariocolax* (*Streblonema) aecidioides* causes tissue thickening in the commercially valuable alga *Undaria* sp. (Yoshida and Akiyama 1979), and *Streblonema*-like endophytes are known to produce galls in some algal hosts (Andrews 1977; Apt 1988a).

Estimates of economic losses for Japan and Korea (Gachon et al. 2010) are estimated at about 10% of the annual production (0.15 billion US dollars globally), mostly due to the oomycete pathogens *Olpidiopsis* spp. and *Pythium* spp. (Ding and Ma 2005; Park et al. 2000). However, spatial and interannual variability feature dramatic variations with reductions of 15–20% and 20–30% in yields and value, respectively, in South Korea and losses in Japan rose to 64% in 1993 (Gachon et al. 2010).

Removal of epiphytes can be carried out by physical (mechanical brushing, rapid water movement), chemical (rinsing in chlorine, copper, or changes in pH), and biological means (use of epiphyte herbivores). However, type III to type V epiphytes (see above), as well as endophytes and eukaryotic parasites, cannot be controlled by such treatments and alternative methods based on the current understanding of the genetic and biochemical basis of close associations are required in order to limit their impacts on algal mariculture. Interestingly, a recent study showed that dipping of seedlings in a commercial extract from *Ascophyllum nodosum* (AMPEP), prior to out-planting, was efficient for both improving the daily growth rate and increased productivity of both varieties of *Kappaphycus* and could be used as part of a management protocol to control or reduce the impact of *Neosiphonia* infection in commercial cultivation areas in the sea (Borlongan et al. 2011).

11.4.3 Fouling

The negative effects of intimate associations on macroalgal fitness can be expected to exert a strong pressure of selection for efficient antifouling defenses. Chemical resistance against various epibiotic organisms, e.g., bacteria, microalgae, periphyton, fungi, invertebrate larvae, and epiphytic macroalgae, has been tested for all major macroalgal groups (worth 1.5 billion US dollars globally reviewed in Davis et al. 1989; Steinberg and deNys 2002; Lane and Kubanek 2008).

Although a wealth of examples on antifouling properties of algal extracts exists, the generality of antifouling metabolites has been questioned. The problem with most of the existing studies is that, although they clearly show macroalgae commonly containing metabolites with antifouling properties, it is not known whether the compounds have an antifouling role in the real ecological interaction with their natural enemies (Steinberg et al. 2001; Dworjanyn et al. 2006). The metabolites may have evolved in other contexts, e.g., as antiherbivory compounds, and their antifouling properties may be artifacts generated by breaking up the cell structure and exposing the compounds to fouling organisms. For example, in the red alga *Delesseria sanguinea*, crude extracts decrease settlement in assays where substrates are coated with metabolites even though the intact alga does not inhibit settlement (Nylund and Pavia 2003).

Although the ecologically relevant examples of natural antifoulants are still few, their number is increasing (Lane and Kubanek 2008), indicating that chemical characteristics of macroalgae do affect the epibiotic community. Further understanding of the ecology and evolution of macroalgal antifouling strategies has become increasingly important (Callow and Callow 2011). When a trait provides resistance to biofoulers in nature, it is realistic to assume that the trait has evolved under selection generated by the epibiotic organisms and such adaptation is susceptible of inspiring biomimetic approaches to design new antifouling strategies.

11.5 Summary and Prospects

Altogether, the data described earlier indicate that marine plants are not passive participants in epibiotic interactions and that they can actively alter their susceptibility to various attackers. Macroalgae produce allelopathic metabolites that act against sessile invertebrates, canopy-forming macroalgal competitors, and epibiotic organisms in particular. Although a large body of evidence that shows that algae are endowed with chemical defenses has been available for some time, the idea that many of these defenses are induced following challenge by bioaggressors has emerged only recently. Consequences of epi/endobiotism to the host alga depend also on the community composition and, vice versa, epibiotism may modify the susceptibility of the host to herbivory. However, relatively few studies have tested the responses in ecologically relevant contexts. The scarcity of epidemiological studies in natural populations of algal species is a major gap for the understanding of naturally occurring mechanisms impacting ecosystem functioning. Hopefully, metagenomics and qPCR approaches open the possibility of scoring the presence and relative abundance of several epiphytes and pathogens in parallel, in order to determine the global pressure acting on natural algal populations. A major challenge, which remains for further understanding, is to address whether fouling pressure and pathogen attacks act as a selective force driving population divergence. An approach that could be applied will be to compare the expression of defense-responsive genes in natural populations experiencing different fouling intensities or infectious diseases. Low cost and more accessible Next Generation of Sequencing methods for monitoring gene expression (RNAseq) will help to identify gene networks and the interplay of defense pathways in a growing number of ecologically and/or economically relevant algal models in response to specific pests. Therefore, patterns of differential gene expression will be assessed and will allow identification of major defense-responsive genes whose expression varies in a population-dependent manner. This will link population genetic variation in stress responses with identification of traits under possible selective pressure. The future for these integrated studies includes molecular genetics, microarrays, proteomics, RNAi assays, and knockouts on a limited amount of marine model algae, combined with a quantitative organismal approach.

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Chapter 12
Invasive Marine Seaweeds: Pest or Prize?

Nikos Andreakis and Britta Schaffelke

12.1 Introduction

In recent decades, nonindigenous marine species (NIMS) have become noticeable features of coastal ecosystems worldwide as well as a major environmental problem and a symptom of global change (e.g., Rilov and Crooks 2009; Sellers et al. 2010). The accelerated occurrence of new marine invasions is a function of intensified maritime traffic, coupled with changing environmental conditions in the "recipient" ecosystems. The latter factor may improve the competitiveness of new arrivals in well-established native communities. Transport by ships is the major vector moving marine biota around the globe, mainly via ballast tanks and biofouling on ships' hulls (Flagella et al. 2007). However, the long-range movement of NIMS is also associated with other marine industries such as aquaculture, fisheries, and marine tourism (Hewitt et al. 2009a; Minchin et al. 2009). Global climate change and other regional stressors such as overexploitation of marine resources, marine habitat fragmentation, and coastal pollution are altering the "recipient" ecosystems. This may provide both available space and a suitable ecophysiological window for survival and establishment of NIMS outside the species' native distribution range, or may reveal species' biological traits that are responsible for "invasiveness." Unfortunately, modeled estimates indicate that the rate of biological introductions will continue to increase, in proportion with increasing global trade and economic development (Lin et al. 2007; Meyerson and Mooney 2007). Now and in the future, a major challenge will be to achieve improvements in (1) the early detection of NIMS, (2) the prediction of ecological and socio-economic impacts, and (3) environmental policy and management to prevent new and to control established introductions of NIMS (Lodge et al. 2006; Costello et al. 2007; Rilov and Crooks 2009).

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Macroalgae represent approximately 20% of the world's marine introduced species. High-profile seaweed taxa such as *Caulerpa taxifolia* (Vahl) C. Agardh, *Codium fragile* (Suringar) Hariot ssp. *tomentosoides* (Van Goor) Silva, *Sargassum muticum* (Yendo) Fenshold, and *Undaria pinnatifida* (Harvey) Suringar have led to well-documented economic and ecological consequences in their introduction range (Schaffelke et al. 2006; Schaffelke and Hewitt 2007; Williams and Smith 2007). Following establishment, these species are able to directly affect the habitat profile by monopolizing space and acting as ecosystem engineers and can significantly modify the composition of local communities by altering competitive interactions and trophic networks (Wallentinus and Nyberg 2007).

Terms such as "pest" or "invasive" are often used to describe introduced taxa. A "pest" has been defined as an introduced species with a documented negative economic effect (Williamson and Fitter 1996), while an "invasive species" spreads rapidly from its point of introduction and becomes highly abundant (Kolar and Lodge 2001). In this book chapter, we mainly use the term "invasive" because the economic consequences, and hence the pest status, of an introduced species are generally not well understood (reviewed in Schaffelke and Hewitt 2007).

Global climate change plays a pivotal role in the perpetuation and evolution of organisms and populations, for example, by slowly changing ecological niches and triggering evolutionary events at the species and population levels (Howden et al. 2003; Mainka and Howard 2010). However, it is difficult to predict how climate change will influence species introductions in the near future (Occhipinti-Ambrogi 2007). For instance, changes in environmental conditions may turn a species into an invasive species in its introduced or even in its native range by revealing certain biological traits of that species that were previously not expressed and confer invasiveness (Mueller and Hellmann 2008; Willis et al. 2010). Conversely, environmental changes may decrease the suitability of the ecosystem for newly established or even well-adapted invasive marine species (Mainka and Howard 2010). Although population growth and dispersal potential can be modeled, it is nearly impossible to predict whether a newly introduced species will become invasive, or where and when.

12.2 Biological Traits of Invasive Seaweeds

Seaweeds are good candidates for becoming invasive given their potential to survive long-range relocations via maritime transport (Flagella et al. 2007; up to intercontinental scales; see also Chap. 17 by Rothhäusler et al.) and because many species have a set of biological traits that make them highly competitive. Functional traits that are recognized to facilitate successful invasions include:

1. High growth rates and in some cases large individual sizes (most invasive green and brown macroalgae are larger than their native counterparts)
2. Vegetative propagation (e.g., red and green invasive macroalgae such as *Kappaphycus* sp., *Ulva* sp., *Caulerpa* sp.)
3. Spectacular growth strategies (e.g., invasive species such as *Caulerpa* spp. form dense covers of siphonous single-cell individuals several meters long and inhabit

a larger depth range than native species; canopy-forming *Sargassum muticum* reduces native biodiversity in invaded areas)

4. High levels of sexual reproduction and high fecundity (e.g., in the invasive lineage of *Asparagopsis taxiformis*)
5. Parthenogenetic reproduction and broad environmental tolerances (*Codium fragile* ssp. *tomentosoides*)

A quantitative ranking of European introduced and native seaweed species (using comparisons of categories of biological traits such as dispersal capabilities, environmental tolerances, reproductive mode, and size) indicated clearly that introduced species with a number of these biological traits have an increased likelihood of being a successful invader (Nyberg and Wallentinus 2005). In some cases, however, the biological traits identified in important invasive seaweeds are also present in noninvasive co-specific or co-generic relatives (Paula and Eston 1987; Trowbridge 1996; Chapman 1999; Vroom and Smith 2001).

Rapid micro-evolutionary changes are common in invasive species because introduced populations are often subject to founder effects and population bottlenecks, have higher incidence of hybridization (suggested to provide innovative genetic variants), and are exposed to a range of novel selective pressures encountered in the introduction range (Brown and Marshall 1981). Acclimatization, adaptation, and thereafter phenotypic modification may arise in response to new biotic (e.g., competitors, consumers, or parasites) and environmental conditions and the drivers of the functional changes are likely to be genetic (reviewed in Whitney and Gabler 2008). However, the question remains whether well-established gene regulation mechanisms, already present in the genome's background, are simply activated by the local selective pressure or the aforementioned changes are the result of a de novo genomic response.

Published accounts suggest that only a limited number of biologically distinct species within algal orders or just one ESU (evolutionary significant taxonomic unit); among a number of cryptic ESUs within the same morpho-species become suddenly invasive. In plants, the switch to invasiveness has been recently related with differences in ploidy levels suggesting that genetic attributes such as polyploidy and high chromosome counts may be the drivers for this transformation (endangered plants exhibit disproportionally low levels of ploidy and chromosome numbers compared to invasive plant species; Pandit et al. 2011). Similar to hybridization, polyploidy may lead to the production of novel and greater numbers of genetic variants, which increases the probability of a successful invasion. An association between polyploidy and invasiveness has been reported in the red alga *Asparagopsis taxiformis* (Andreakis et al. 2007b, 2009) and should be further explored in other invasive marine algae, given the general propensity for polyploidy in seaweeds (based on nuclear genome size estimates; Kapraun 2005).

It has been debated whether ecosystems exhibiting high species richness are less vulnerable to biological invasions because in theory only a limited, highly specialized, number of empty niches are available for the invader. Furthermore, it has been assumed that polluted "recipient" environments are likely to promote invasive traits in NIMS (Davis et al. 2000; Davis and Pelsor 2001; Dunstan and Johnson 2007; Valentine et al. 2007; Whitney and Gabler 2008). In addition, invasion attempts are more likely to be successful when the environmental conditions in recipient ecosystems are similar to conditions in the ecosystem the invader has evolved. In the latter case, the chances of survival and establishment of invasive seaweeds following introduction are often improved because their natural enemies such as herbivores or parasites are not introduced with them (i.e., the enemy release hypothesis; Cacabelos et al. 2010; Engelen and Henriques 2011). This means that the energy invested into defense in their native environment (e.g., grazing resistance; see Chap. 8 by Iken) can now support growth and biomass production, increasing the competitiveness of the introduced species.

For a successful invasion, biological traits such as broad ecophysiological tolerance and the consequences of differential gene expression are likely to act in synergy under sufficient inoculation pressure and favorable characteristics of the "recipient" ecosystem. The relative importance of each of these traits, however, is poorly understood because they are likely to be species and location-specific and it is impossible to perform controlled experiments at large biogeographic and evolutionary timescales (Schaffelke and Hewitt 2007).

12.2.1 Seaweed Invasions Are Mostly Human-Mediated

The introduction of a seaweed species often comprises a plethora of immigrants of several genetic variants and ecotypes entering the "recipient" environment. Simplistically, settlement and establishment will be feasible if the species' ecophysiological limits for survival match the environmental conditions in the "recipient" environment. While not fully understood for many individual species, the stages of a successful seaweed invasion have been described as: (1) uptake and transport of propagules, (2) survival and release of propagules and establishment of low-density populations, and (3) increased competition with native biota, spread, expansion, and impact of populations of introduced seaweeds (Schaffelke et al. 2006).

The accidental uptake, transport, and release of propagules into the recipient environment are the only stages of the process when human intervention can prevent biological invasions. Marine seaweeds make use of many vectors for dispersal such as specialized floating structures (see Chap. 17 by Rothäusler et al.), gametes or spores for sexual reproduction, fragments of thalli for vegetative propagation, or attachment to long-distance moving organisms (e.g., sea turtles). The dispersal of most invasive seaweeds, however, is associated with human activities, which could be managed (Hewitt et al. 2009a). Biofouling (i.e., the attachment of the seaweed to any part of a vessel or marine equipment) is one of the most common and also oldest mechanisms of human-mediated relocation of seaweeds. The other main vectors are ballast waters, used to stabilize large vessels for long-distance voyages, that transport algal propagules and intentional relocations of aquaculture species (e.g., as fouling on oyster shells or as packing material) consequently responsible for seaweed introductions (Hewitt et al. 2006).

12.3 The Identification of Introduced Seaweeds Is Not Always Easy

Seaweeds have circumnavigated the globe for centuries. Unintentional introductions by humans have occurred since the beginning of naval explorations and this may explain a perceived "cosmopolitan distribution" reported in many "hull-fouling" species (mostly small, ephemeral species that colonize ship's hulls; Godwin 1975; Ruiz and Carlton 2003). A species' geographic distribution can be misinterpreted especially in taxa with few diagnostic morphological characters (e.g., *Ulva lactuca* Linnaeus, *Bryopsis plumosa* (Hudson) C. Agardh) for the following reasons: firstly, most seaweed taxa have been described from a limited number of geographical regions and/or expeditions; taxonomists in the past relied heavily on these already characterized "type species" to identify new taxa. Secondly, although molecular tools are today able to characterize genealogically distinct units, a significant number of taxonomists still rely on the use of morphological characters for a routine identification of species (Sherwood 2007).

The identification of even well-studied introduced seaweeds is not always straightforward and the assessment of an introduction episode is extremely complex. We will discuss here two important reasons. (1) Due to extreme phenotypic plasticity of many seaweed genera, closely related algal species can be morphologically almost identical and therefore difficult to distinguish. Furthermore, cryptic species with separate geographic distributions have been observed within morphologically homogeneous taxa. Cryptic invasion episodes may therefore occur and are likely to lead to (a) misidentified biologically distinct invasive species due to morphological similarities with natives or (b) misidentified genealogically distinct lineages of invasive character found within a single morpho-species complex. Although forensic techniques may provide the necessary tools to achieve a reliable and quick identification of the invader, results are often compromised by the absence of sufficient DNA sequence data for comparisons and species identification (Box 12.1), even in some phylogenetically important groups of seaweeds (e.g., *Ulva* and *Bryopsis*). Furthermore, a species concept to describe the taxonomical units within these groups is often nonexistent. (2) A large number of species are today recognized as "cryptogenic" (i.e., there is no reliable evidence to indicate whether a species is native or introduced, Carlton 1996); because human-mediated relocations of marine biota have occurred since historical times while archeological or paleontological evidence related to the geographical origins of many soft-body marine organisms is largely absent. A number of biogeographical criteria have been proposed to distinguish between native and introduced taxa (Geller et al. 2010) and a species' cryptogenic history can be resolved in some cases where biological invasions have been systematically studied, e.g., *Ulva flexuosa* Wulfen cited as *Enteromorpha lingulata* J Agardh, *Caloglossa leprieurii* (Montagne) G. Martens, *Bostrychia radicans* (Montagne) Montagne in southern Brazil (Neves and Rocha 2008).

The effective management of a biological invasion requires a solid knowledge of (1) which species has been introduced, (2) the source of the introduction, and (3) the

Box 12.1

Two main approaches are used to identify the source of NIMS. The first relies on the assumption that the vector of introduction (e.g., ballast waters of cargo ships along a specific route) is known. Knowledge of the target species' distribution range and the navigation routes can be combined to identify the likely source regions for that species. Vector management can then prevent further introductions (Ruiz and Carlton 2003). Most importantly, biogeoclimatic models can forecast potential zones vulnerable to invasion and predict the range expansion of invasive NIMS by combining information gathered from species distribution, transport vectors, local ecophysiological conditions, and the species-known ecophysiological tolerance ranges (Arrontes 2005).

A second method deploys DNA sequencing markers and geographical information (phylogeographic approach). Specimens are collected, DNA is extracted, and the same (one or more than one) DNA region is sequenced from multiple individuals to infer the genealogical relationships among introduced and putative native populations of the invasive species and reconstruct the spatial history of the invasion (Fig. 12.1). A variety of DNA sequencing markers have been today developed from mitochondrial, plastid, and nuclear genomes (see case studies); however, the successful use of the approach relies on the resolution of the marker and an adequate sampling strategy. Less applied in seaweed invasion biology is the population genetic approach based on allele frequencies of microsatellite markers to assign individuals to a specific population (for reviews of both approaches, see Wares et al. 2005; Muirhead et al. 2008).

extent of the introduced range. This information can be immediately available where algal floras are well described and survey programs for early detection are in place (Anderson 2007). In geographical regions, however, where local seaweed species are poorly explored and historical records such as species lists are limited, a presumably introduced species may either be native or cryptogenic. Visual surveys and identifications based on gross morphology are often sufficient to detect introductions since many NIMS are conspicuous and genetic discontinuities do not always occur within species (O'Doherty and Sherwood 2007; Castelar et al. 2009). However, many algal genera have extreme levels of phenotypic plasticity and species can potentially hybridize with close relatives (e.g., introduced and native populations of *Fucus evanescens* and *F. serratus*; Coyer et al. 2007). For many introduced seaweeds only multidisciplinary approaches, which take into account molecular, morphological, reproductive, and ecophysiological evidence, are able to characterize the introduced taxonomic units. Such approaches provide sound information on the origins and the geographical trajectory of the invasion and are able to predict persistence and expansion potential of introduced populations (Flagella et al. 2010; Pang et al. 2010).

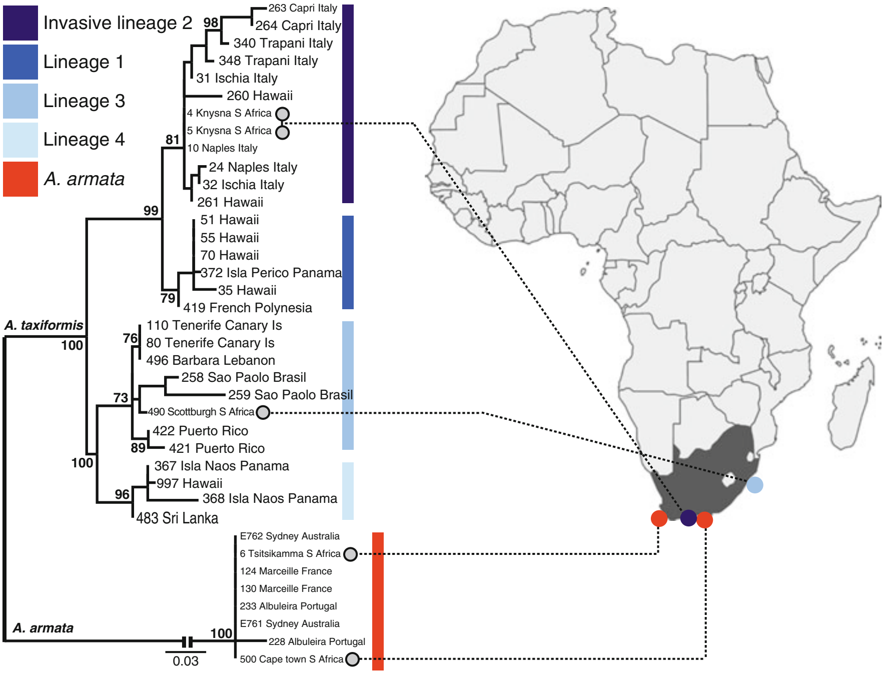

Fig. 12.1 Molecular phylogeographic approach modified from Bolton et al. (2011) to elucidate multiple cryptic introductions of morphologically nearly identical lineages and species (gametophytes and tetrasporophytes) of the red seaweed genus Asparagopsis from specimens collected in South Africa. Both the Indo-Pacific lineage 2 of *A. taxiformis* and *A. armata* constitute notorious invasive species. The highly informative mitochondrial *cox*2–3 intergenic spacer has been deployed in this case. Sequences from previously identified specimens belonging to the five ESUs, collected worldwide and of known origin, are merged with sequences from specimens collected in the study area (*gray circles*) to produce a robust phylogeny and reproduce the two-species genealogical history. From the latter, the identity of each of the target cryptic specimens is revealed. The superimposed geographical information on the phylogram will indicate "which target ESU is where." The level of sequence similarity between sequences of known geographical origin and the target sequences will indicate the source population. Following analyses, unclassified specimens (*gray circles*) are successfully identified (*colored circles*) at the species and lineage levels; lineages and species are finally associated with a geographical location

12.3.1 Relevant Taxonomic Units in Seaweeds Molecular Ecology

Levels and patterns of local marine biodiversity fluctuate, in part due to the exchange of biota among bioregions. In recent years, however, remarkable changes in biodiversity have been revealed at the subspecies level. Molecular techniques in algal systematics are critical to define new relevant units of biological organization for ecological surveys and biodiversity estimates (Box 12.1). These taxonomic units in the vast majority of the cases do not correspond to the traditional species concept (Biological species concept; sensu Mayr 1942) but are recognized within molecular phylogenies as genetically distinct, statistically robust, reciprocally monophyletic clades (Evolutionary Significant Units, ESUs, sensu Moritz 1994; Wattier and Maggs 2001; Provan et al. 2005; Uwai et al. 2006a; Stam et al. 2006; Andreakis et al. 2007a; Verbruggen et al. 2007). The condition of monophyly represents a key assumption for biological classification of organisms; monophyletic clades herein include an organism and all its descendants. ESUs may correlate with geographical distribution and common morphology. Overall, ESUs respect the phylogenetic species concept and are characterized by distinct evolutionary trajectories although the possibility of interbreeding is not excluded.

In the context of invasion biology, ESUs are intended as suitable taxonomic units to elucidate invasions and represent terms such as strains, haplo-groups, lineages, or varieties, conventionally used to express the level of genetic variation and explain the phylogeographic patterns found in introduced seaweeds. The number of uncovered ESUs can vary significantly between studies and largely depends upon the resolution and the speed of “lineage sorting” of the molecular marker used. This is because molecular marker systems are characterized by variable levels of evolutionary speed, distinct genealogical trajectories, and/or uneven intensities of selective pressure; these are all characteristics accounting for the heterogeneity in a phylogenetic signal and its resolution. Therefore, independent information for more than one DNA region and ideally from distinct genomes (nuclear, mitochondrial, and plastid) is necessary to achieve consistent results for delineating ESUs and inferring phylogenies at the sub-species level.

In the last decades, DNA barcoding has been largely used in plant and animal systematics. The method involves sequencing and similarity analysis of a short fragment of DNA from multiple specimens, corresponding to a highly conserved region in the genome such as the subunit one of the mitochondrial gene cytochrome *c* oxidase (COI; Blaxter 2003). However, information coming from a single, extremely short DNA region, compared to the size of a genome, is far from being reliable in modern phylogenetics. This is particularly true in (1) groups of organisms with limited sequence diversity, (2) recently diverged species, (3) hybrids (i.e., offspring of parents belonging to biologically different species, and (4) pseudogenes (i.e., nonfunctional DNA sequences resembling functional genes). The need to employ in a single assay more than one universal biological marker in organism classification can today be satisfied by the increasingly growing number of completely sequenced prokaryotic and eukaryotic genomes. At present, techniques such as DNA microarrays or DNA chips represent the most powerful way to gather as much information as possible from a single individual genome in a single trial in a cost-effective way. In the future, the latter techniques and improvements therein, in combination with advances in data processing and computation power, will permit the inference of phylogenetic relationships among taxonomically robust taxa, ideally at the whole-genome level based on the analysis of their full set of genes (Garzon and Wong 2010).

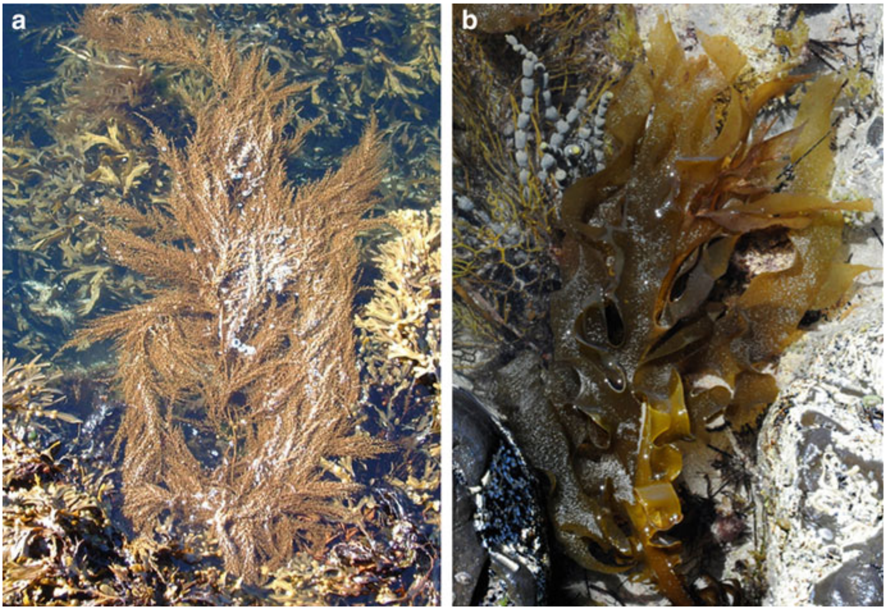

Fig. 12.2 (**a**) *Sargassum muticum* (photo by Stefan Kraan); (**b**) *Undaria pinnatifida* (Harvey) Suringar (Algaebase, image Ref. 15830, photo by Mike Guiry)

12.3.2 Case Study: Sargassum Muticum

The large brown Japanese seaweed *Sargassum muticum* (Yendo) Fensholt (Fig. 12.2a) is one of the most invasive and widely established algae in Europe and North America (Monteiro et al. 2009; Kraan 2008). Contrary to other brown macroalgae (such as *Undaria pinnatifida* and *Fucus serratus*) no evidence for genetic differentiation has been detected between native Asian and introduced populations in this species. This indicated a number of recent invasion events supported mainly by the transport of Pacific oysters introduced for farming in Canada, UK, and France. Nuclear (ITS2; internal transcribed spacer 2) mitochondrial (*Trn*W-*Trn*I spacer) and plastid (RUBISCO spacer) markers failed to uncover significant levels of DNA polymorphisms in *S. muticum* individuals collected globally, which would be required for the reconstruction of the genetic identity of invasive and native populations in this species. The low levels of genetic variability encountered in the native and introduced range of *S. muticum* together with previous morphological confusions with closely related species prohibited the identification of the source populations and the direction of the introduction episodes along the invasion pathway of this important invasive seaweed (Cheang et al. 2010).

12.3.3 Case Study: Undaria Pinnatifida

The brown seaweed *Undaria pinnatifida*, known as the edible *wakame* (Fig. 12.2b), was originally endemic to Japan, Korea, and China where it is industrially cultivated. Firstly observed outside its native distribution range in the Mediterranean Sea (Etang de Thau, French, 1970s) the species has in few years invaded many of the world's oceans from Europe to North America, Australasia, and New Zealand; both by accidental translocation via oyster farming from Japan and intentional introduction for cultivation purposes (Voisin et al. 2005). It was possible to explore and elucidate the invasion history of this species by means of sequence analysis of the mitochondrial *atp*8-*trn*S and *trn*W-*trn*I intergenic spacers, the partial *cox*3 gene and the *tatC-tLeu* gene regions. The latter DNA loci revealed highly differentiated populations, each characterized by low levels of haplotype diversity in the native geographical range of the species (Voisin et al. 2005). On the contrary, where *U. pinnatifida* has been introduced, populations were found to be highly diverse. The so distributed genetic diversity clearly indicated that introduced populations of *U. pinnatifida* are the results of multiple introduction events from more than one native population. Furthermore, the difference in haplotype diversity found in introduced populations sampled from Europe and Australasia indicated differences in the dynamics of the colonization process (Voisin et al. 2005; Uwai et al. 2006a, b).

12.3.4 Case Study: Asparagopsis Armata

The red seaweed *Asparagopsis armata* Harvey (Fig. 12.3a) is a genetically homogeneous species originally described from Southern Australia, Tasmania, and New Zealand and first reported in the northern hemisphere from Algeria in 1925 (Horridge 1951). Molecular phylogenies inferred from the D1, D2, and D3 hyper-variable domains of the nuclear large subunit rDNA gene the plastid RUBISCO spacer and the mitochondrial cox2–3 intergenic spacer indicated just a single plastid haplotype distributed worldwide and a limited number of panmictic nuclear and mitochondrial haplotypes in presumably native and introduced populations. *Asparagopsis armata* exhibits great dispersal potential due to a free-floating tetrasporophyte in its life cycle (see below) and propagation via fragmentation and attachment to other floating structures and has always been reported as a recently introduced, potentially invasive, species from the Mediterranean Sea and western European coasts. Given the complete absence of phylogeographic structuring on global and local scales and the inadequate phylogenetic signal of nuclear, mitochondrial, and plastid markers, only general assumptions on the origins of introduced populations and the direction of the spread can be made. Furthermore, significant taxonomic confusion surrounds this species and has been propagated since its first description. This is because no diagnostic morphological characters are known to differentiate between tetrasporophytes (the "*Falkenbergia*" stage, previously described as separate species)

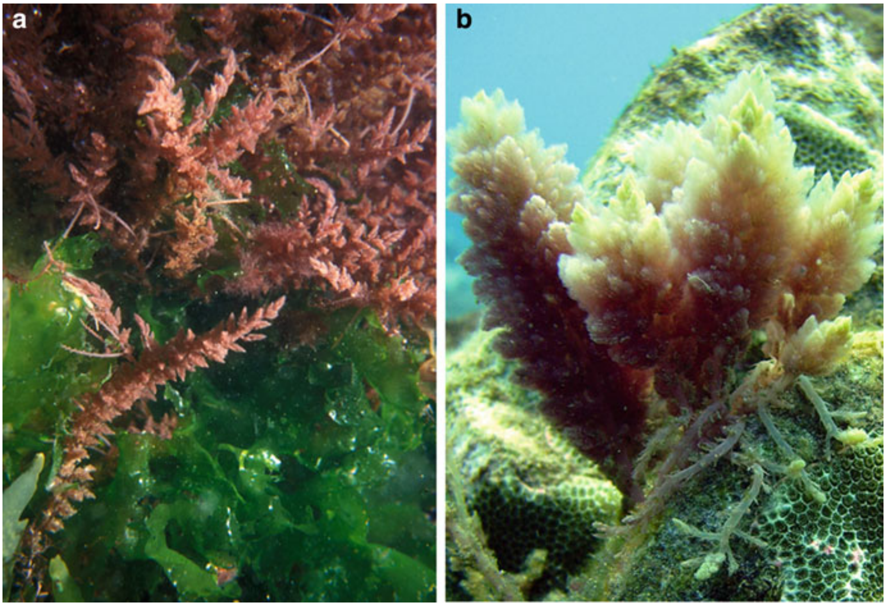

Fig. 12.3 (**a**) *Asparagopsis armata* on *Ulva* (photo by Stefan Kraan; (**b**) unidentified lineage of *Asparagopsis taxiformis* (photo by Mark JA Vermeij)

of *Asparagopsis* species. Although it is easy to identify the macroscopic *A. armata* gametophytes in the field, the identification of cryptic Falkenbergia isolates and their assignment to *A. armata* populations is only feasible with molecular tools or by inference when *Asparagopsis* gametophytes and *Falkenbergia* occur at the same sites.

12.3.5 Case Study: Asparagopsis Taxiformis

The warm temperate to tropical red seaweed *Asparagopsis taxiformis* (Delile) Trevisan de Saint-Léon, 1845, (Fig. 12.3b) consists of four genetically distinct yet morphologically virtually identical mitochondrial lineages, detectable only by molecular tools (the nuclear D1, D2, and D3 hyper-variable domains of the large subunit rDNA gene, the plastid RUBISCO spacer, and the mitochondrial cox2–3 intergenic spacer). One of these, lineage two, is of Indo-Pacific origin and invaded the Mediterranean basin from the Suez Canal (Ní Chualáin et al. 2004; Andreakis et al. 2004, 2007a, b). Phylogeographic patterns inferred from individuals of this species-complex collected globally were suitable to delineate cryptic taxa, infer lineage-specific distribution patterns, and elucidate single or multiple introduction events worldwide. Most importantly, the phylogeographic approach was useful to distinguish between native and invasive cryptic taxa where more than one lineage was found in sympatry. For instance, lineages 1, 2, and 4 co-occur in the Hawaiian archipelago [lineage 2 is considered native and lineage 4 introduced to the islands as recently as in 1991 (Sherwood 2008)]. Lineages 1 and 4 co-occur sympatrically within hundreds of meters in the Pacific side of the Isthmus of Panama and they may represent multiple introduction events. Lineages 2 and 3, the latter of Atlantic distribution, are found in South Africa and are considered introduced and invasive, respectively (Bolton et al. 2011).

Individuals with a *A. taxiformis* morphology collected in unrelated geographic locations have in the past been described as separate species. This observation, together with the multiple ESUs found in *A. taxiformis*, strongly suggests that the taxonomic status of the species sensu stricto needs to be revisited. For instance, one of these lineages may correspond to *A. svedelii* W.R. Taylor (1945), an endemic taxon of the Galápagos Islands, considered synonymous to *A. taxiformis* (Taylor 1945), while cryptic lineage 2 may correspond to *A. sanfordiana* Harvey (Setchell and Gardner 1924), another species considered to be a synonym of *A. taxiformis*.

12.3.6 Case Study: Codium Fragile *ssp.* Tomentosoides

A single strain of the green alga *Codium fragile* sensu stricto known as *Codium fragile* ssp. *tomentosoides* (Fig. 12.4a) is recognized as highly invasive. DNA sequence analysis based on plastid microsatellites and the plastid *psb*J-*psb*L, *rpl*16-*Rps*3, and *trn*G(UCC)-5 S DNA regions of individuals collected throughout the strain's known native and introduced distribution range indicated extremely low levels of genetic variation with only four distinct haplotypes encountered in Japan where the strain occurs naturally. Despite the limited levels of genetic variability, the phylogenetic signal was sufficient to uncover at least two separate introductions in the biogeographic history of *C. fragile* ssp. *tomentosoides*: two of these haplotypes were highly structured geographically and were found in introduced populations, one exclusively in the Mediterranean Sea, and the other exclusively in Northwest Atlantic, Northern European, and South Pacific populations (Provan et al. 2005, 2008).

12.3.7 Case Study: Caulerpa *spp.*

The green algal genus *Caulerpa* comprises morpho-species complexes, species that may become invasive under certain conditions and ESUs known from the literature as "invasive strains" (e.g., described in *C. taxifolia* sensu stricto*)* or "invasive varieties" [e.g., described in *C. racemosa* (Forsskål) J. Agardh sensu stricto (Stam et al. 2006)]. For instance, a potentially invasive species, *Caulerpa prolifera* (Forsskål) J.V. Lamouroux*,* is widely distributed in tropical and subtropical seas and has been significantly altering the structure and functioning in its introduced

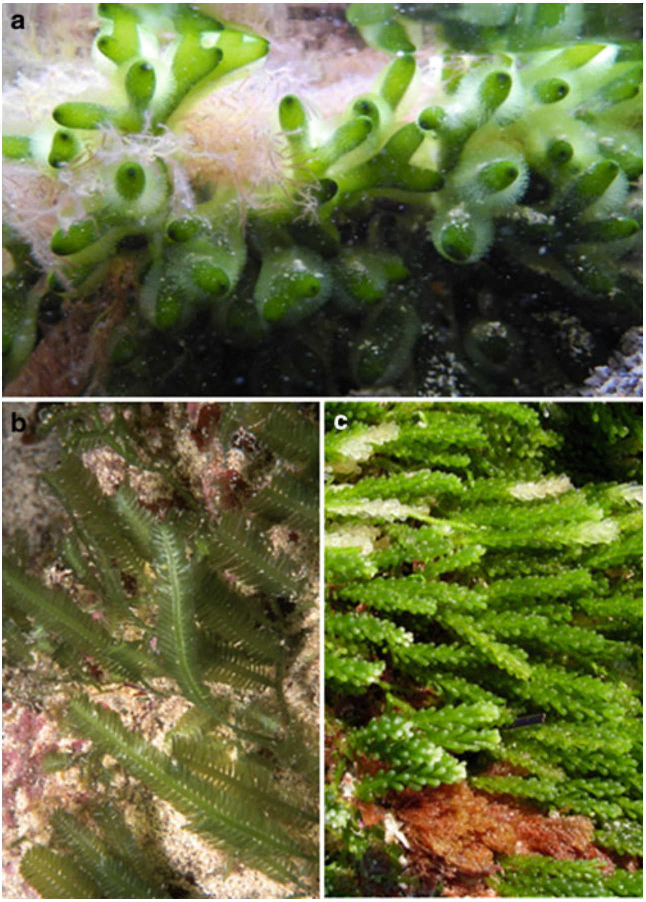

Fig. 12.4 (**a**) *Codium fragile* subsp. tomentosoides (van Goor) P.C.Silva (Algaebase; image Ref. 17373, photo by Mike Guiry); (**b**) *Caulerpa taxifolia* (photo by John Huisman); (**c**) *C. racemosa* var. cylindracea (Sonder) Verlaque, Huisman and Boudouresque (photo by John Huisman)

habitats (e.g., Gab-Alla 2007). The widespread tropical/subtropical seaweed *Caulerpa taxifolia* (Fig. 12.4b), native to the Atlantic, Indian, and Pacific Oceans, was the first seaweed invasion to draw widespread public attention after its introduction to the Mediterranean Sea in the 1980s, its fast spread, and well-documented negative ecological impacts (reviewed in Schaffelke and Hewitt 2007).

Nuclear molecular phylogenies inferred from sequences of the rDNA-ITS1 + 2 region (ribosomal DNA—internal transcribed spacer 1 and 2) from hundreds of *Caulerpa* individuals collected worldwide were used to delineate species, "varieties," and "strains" of problematic morphological identification. The global phylogenetic reconstruction contributed to the identification of the invasive "aquarium strain" of Australian origin of *C. taxifolia*, which has been introduced at various locations worldwide (Stam et al. 2006). *Caulerpa taxifolia* sensu stricto cannot be distinguished morphologically from this invasive ESU which, following accidental introductions, has successfully established in temperate areas such as the United States, Mediterranean Sea, and southern Australia. Eradication attempts in Australia and the United States (the latter seems to have been successful) and an international ban of this species in the aquarium trade were the initial management responses (Anderson 2007).

The same nuclear marker has been successfully used to uncover the now well-known invasive variety of *Caulerpa racemosa* (*C. racemosa* var. cylindracea (Sonder) Verlaque, Huisman and Boudouresque; Fig. 12.4c) against two other morphologically similar, and apparently noninvasive, sister varieties within the introduced range of the *C. racemosa* complex (*C. racemosa* var. *turbinata–uvifera* (C. Agardh) J. Agardh, *C. racemosa* var. *lamourouxii* (Turner) Weber-van Bosse f. *requienii* (Montagne) Weber-van Bosse; varieties reviewed by Klein and Verlaque 2008). The approach was particularly useful in the Mediterranean basin where other *C. racemosa* varieties have been erroneously misidentified as the invasive variety (Verlaque et al. 2003, Yeh and Chen 2004; Nuber et al. 2007). Although the invasive lineage represents a dominant algal component in the Mediterranean basin, its identity has been definitely confirmed by combining morphological and molecular data in only five of the 13 Mediterranean countries in which *C. racemosa* sensu stricto has been reported so far (France, Italy, Greece, Croatia, and Cyprus; Klein and Verlaque 2008). This ESU has been introduced into the basin from south-western Australia. Due to its well-documented negative ecological impact, this invasion is considered as one of the most serious biological invasions in the history of species introduced into the basin (Klein and Verlaque 2008).

12.3.8 Assessing Seaweed Introductions

In recent years, several conspicuous seaweed invasions have been detected. Our case studies illustrate that introduced seaweeds may be either genetically homogeneous or species consisting of multiple cryptic lineages.

Populations of taxa in the former category are characterized by weak phylogenetic signals and insufficient phylogeographic structuring between the native and introduced geographical range of the invasive species. Such introduced species are only easy to detect based on morphology if detailed floristic records exist in a particular region. It is however impossible to identify the source populations and the subsequent direction of the invasion based on either morphological identifications or genetic approaches.

Morphologically cryptic species often occur within so-called widely distributed taxa characterized by large geographic disjunctions and apparently low levels of connectivity among populations. The morphological delineation of these ESUs is often impossible even for the expert taxonomist; most importantly, it is difficult to distinguish between a recent introduction and the tendency of the species to disperse naturally (the latter may have occurred in timescales of hundreds to thousands of years before present). However, a molecular phylogeographic approach may represent a sufficiently robust strategy to delineate the cryptic taxa and, most importantly, provide information on the origins of the invader and the direction of the invasion process (see Box 12.1; Voisin et al. 2005; Andreakis et al. 2007a, b; Sherwood 2008).

When cryptic taxa remain unrecognized, significant evolutionary and ecological changes of the local marine biodiversity at the subspecies level will remain unknown. Most importantly, cryptic invasions generally escape the critical management mechanisms of early detection, control, and future prevention. Conversely, if cryptic taxa are misidentified, the impacts of invasions can be erroneously overestimated due to the co-occurrence of morphologically similar invasive and noninvasive cryptic ESUs belonging to the same species-complex.

The increased recognition of cryptic ESUs has significantly changed our view of distribution, abundance, ecophysiology, and conservation status of seaweed species. In the light of the high rate with which new ESUs are discovered, firstly, the taxonomic status of several so-called cosmopolitan species has to be reconsidered. Secondly, the newly emerging patterns can be used to formulate hypotheses on diversification rates and to discover biodiversity hotspots. Thirdly, and most importantly, results are essential to develop accurate assumptions on extinction risks and population sizes. Marine science in the post-genomic period with hundreds of genomes sequenced so far requires a convincing yet suitable taxonomic unit. This is of crucial importance to corroborate ecological, biological, and evolutionary interpretations, but also for practical applications such as management of Marine Protected Areas and active bio-invasion control programs.

12.4 Are Introduced Species a Pest or Prize? A Crab's Tale

The Chinese mitten crab is native to the rivers and estuaries of the Yellow Sea in Korea and China, and has been introduced to many regions of the world. The two quotations below illustrate the *conundrum* whether this crab species is a pest or a prize. Counting the number of scientific publications on this species (ISI web of Knowledge, viewed 05 April 2011) suggests the latter, as most publications report on aspects of economic use, e.g., reproductive performance and breeding optimization.

"*The Chinese mitten crab (*Eriocheir sinensis*) is considered one of the world's top 100 invaders by the Invasive Species Specialist Group (ISSG), part of the Species Survival Commission of The World Conservation Union (IUCN). Populations of* E. sinensis *have recently become established on the west coast of the U.S. and now pose a potential threat to the native fishes and invertebrates and to freshwater and brackish estuarine communities*" (Dittel and Epifanio 2009).

"*The Chinese mitten crab (Eriocheir sinensis) is one of the most important cultivated aquatic species in northern China. Significant advances have been made in the crab farming during last years due to its "high market value with* *declining yields. (...) The annual production of crabs has reached more than 400,000 t valued more than 20 billion RMB in 2005 in China*" (Li et al. 2007).

The food on our tables today comes mostly from a small number of widely cultivated plant and domesticated animal species. Most of them are historical intentional introductions. For example, the earliest archeological records of agriculture in India 2400–1750 BC show crop species of west Asian origin (Hutchinson 1976), while the transport of crop species between Europe, Africa, and Asia peaked with the establishment of direct intercontinental sea trade in the 1400s (National Research Council 1996). There is no evidence that the main crops, such as cereals, oil seeds, fruits, and vegetables, were invasive in their native range. However, over the last 10,000 years modern cultivars (from "*culti*vated *var*iety") have been continuously selected for maximum performance in a range of environments. In addition, modern farming practices such as fertilization, irrigation, crop rotation, the use of pesticides, and genetically assisted breeding have provided extraordinary growth rates and production of high biomass. Interestingly, many invasive seaweed species or ESUs fit the profile of successful agricultural cultivars because they exhibit evolutionary traits for e.g., fast growth, high reproductive capacity, grazing resistance, and wide ecophysiological tolerances to persist in different environments.

12.4.1 Commercially Used Invasive Seaweeds

Seaweeds have been highly valued food resources for thousands of years, especially in Asia. Today, seaweed harvesting and mariculture is an actively growing global industry with a currently estimated total annual value of approximately six billion USD (McHugh 2003). Seaweeds are used mainly as food products for direct human consumption, sources of bulk chemicals such as hydrocolloids and other higher value biochemical compounds, fertilizers, and animal feed additives (see Chap. 22 by Buchholz et al.). The farming of seaweeds has expanded rapidly as demand has outstripped the supply available from natural resources (McHugh 2003).

Many cultivated seaweed species, harvested in their native range, have been intentionally or unintentionally introduced (reviewed in Schaffelke and Hewitt 2007) and are often highly valued for their invasive traits, especially for fast growth rates and biomass accumulation, and often low levels of epiphytism and resistance to herbivores. The commercialization of invasive seaweeds and the exploitation of species-specific invasive traits are often considered to be positive for the economic development of the regional community (Pickering et al. 2007). However, this has to be balanced with the potential negative side effects on the ecological integrity of the "recipient" environments due to accidental release or escape of invasive species, which are difficult to manage. The following sections present brief summaries of the most important commercially used seaweed species, which are also high-profile invaders.

12.4.2 Gracilaria salicornia

Gracilaria species represent well-recognized sources of linear galactan polysaccharide agar, widely used in industry for its excellent gelling or thickening abilities (reviewed in Mehta et al. 2010). Species of the genus *Gracilaria* such as *Gracilaria salicornia* (C. Agardh) Dawson and *G. parvispora* Abbott, a highly valuable alga in the Hawaiian markets, occur widely throughout the tropical Indian and Pacific Oceans (Ryder et al. 2004). Furthermore, *G. debilis* (Forsskål) Børgesen and *G. salicornia* occur naturally at the west coast of India where they represent valuable natural sources for superior quality agars (Oza and Zaidi 2001; Mehta et al. 2010). Several *Gracilaria* species from various sources were intentionally introduced to the Hawaiian Islands for aquaculture development (Russell 1992). *Gracilaria salicornia* has become a successful invader. After escaping from sea farms, *G. salicornia* has invaded surrounding coral reef flats, either as unattached drift or attached populations outcompeting corals, propagated mainly via fragmentation (Smith et al. 2004; Conklin and Smith 2005). *Gracilaria salicornia* displays a variety of biological traits that facilitate high yield cultivation but also make this a potentially invasive species: e.g., high growth rates that can be sustained in variable light regimes, the ability for vegetative dispersal, desiccation tolerance, remarkable tolerance to a wide range of temperatures, salinities, chemical treatments (commercial-grade herbicides and algaecides), and resistance to herbivores (Rodgers and Cox 1999; Smith et al. 2004; Nelson et al. 2009).

12.4.3 Eucheuma *and* Kappaphycus *spp.*

Wild and farmed strains of the carrageenophytes *Eucheuma denticulatum* (Burman) Collins et Harvey, *Kappaphycus alvarezii* (Doty) Doty and *Kappaphycus striatum* (Schmitz) *Doty ex Silva* have been intentionally introduced in more than 20 countries for mariculture purposes (Bulboa and de Paula 2005; Hayashi et al. 2007). These species represent the world's most important kappa-carrageenan producing red algae (Ask and Azanza 2002), a hydrocolloid that is widely used in industry as a gelling and thickening agent. All, however, have been introduced to Kane'ohe Bay in Hawai'i in 1974 for growth experiments and since then accidentally escaped and established highly abundant populations on Hawaii's coral reefs (Conklin and Smith 2005). However, most introductions for cultivation have occurred in the developing world and adverse impacts on the surrounding environment are not well studied (Zemke-White 2004; Bindu and Levine 2011).

Invasive traits that make these species ideal for farming are easy propagation and dispersal by fragmentation and very high growth rate (doubling in size every 15–30 days). The improvement of growth performance in these species is an area of active research (Luhan and Sollesta 2010).

12.4.4 Asparagopsis *Species*

Gametophytes of *Asparagopsis armata* and *A. taxiformis* represent promising sources of pharmaceutical agents of remarkable anti-protozoan, bactericidal, and fungicidal activities (McConnell and Fenical 1977; Woolard et al. 1979; Paul et al. 2006; Salvador et al. 2007; Genovese et al. 2009). In addition, *Asparagopsis* species produce valuable natural secondary metabolites such as compounds with considerable antimicrobial activity against *vibrio harveyi* strains, useful in cosmetics industry and animal aquaculture (Salvador et al. 2007; Manilal et al. 2009); compounds of cytotoxic activity against cancer cells (Zubia et al. 2009) and as preservatives in industrial applications (Kraan and Barrington 2005). Furthermore, "*Falkenbergia*" stages have been successfully cultivated in southern Portugal and can be used as continuous, rapidly growing bio-filter systems for the effluent of commercial fish farms (Schuenhoff et al. 2006; Figueroa et al. 2008; Mata et al. 2010). Introduced in Ireland in 1939, and following population decline due to inadequate temperature for sexual reproduction, *Asparagopsis armata* is now commercially cultivated. The persistence of this species along the Irish West coast seems to be due to continued replenishment from a single aquaculture operation (Kraan and Barrington 2005).

Both *A. taxiformis* and *A. armata* exhibit a number of invasive traits, including vegetative propagation of gametophytes and tetrasporophytes, frequent sexual reproduction of tetrasporophytes, and a suite of halogenated secondary metabolites that increase resistance to herbivory (Boudouresque and Verlaque 2002; Paul et al. 2006; Williams and Smith 2007). In addition, polyploidy has been associated with the extraordinary invasive success of the Indo-Pacific Mediterranean linage 2 of *A. taxiformis* (Andreakis et al. 2009). Furthermore, "*Falkenbergia*" is particularly well suited to human-mediated transport (ballast water) and capable of surviving for long periods as free-floating or loosely attached filaments transported on ships, animals, and other materials in aquaculture (Flagella et al. 2007).

12.4.5 Caulerpa *Species*

Among three genetically distinct ESUs of the *Caulerpa racemosa* species-complex occurring in the Mediterranean Sea, the so-called *C. racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman and Boudouresque, is highly invasive. *Caulerpa* species are greatly valued for human consumption due to their high vitamin and protein content ("sea grapes", *C. racemosa* var *laetevirens*, *C. racemosa*, *C. geminata*, *C. hodgkinsoniae*) or pleasant taste ("green caviar", *C. lentillifera*) and have been identified in several countries as high-value candidates for cultivation and commercial production (Matanjun et al. 2009). *Caulerpa* species also offer promising potential for bioremediation of nutrient-enriched effluent from intensive tropical aquaculture systems because of their high nutrient uptake rates (linked to high growth rates) and the fact that many *Caulerpa* species are native and sufficiently abundant in regions where aquaculture operations are expanding (Paul and de Nys 2008). The downside of the easy cultivation is that several potentially invasive *Caulerpa* species have been commercialized and can be easily purchased from aquarium shops or ordered online. The aquarium industry has enormously facilitated the transportation of these species to distant geographic locations and hence the potential for introductions into natural habitats with serious ecological consequence (Zaleski and Murray 2006; Stam et al. 2006).

The main invasive traits in *Caulerpa* species are high growth rates, propagation via fragmentation (i.e., 1 cm small fragments of *C. taxifolia* are able to give rise to viable single siphonous-cell three-dimensional structures up to 5 m long), broad environmental tolerances, survival out of the water in humid conditions for several days, and in some cases, such as in *Caulerpa racemosa* and *C. taxifolia,* production of secondary metabolites and allelopathic compounds that act as herbivore deterrents and/or inhibit other floral components during space competition (e.g., Meinesz 1999; Vroom and Smith 2001; Gollan and Wright 2006; Wright and Davis 2006; Klein and Verlaque 2008; Raniello et al. 2007).

12.4.6 **Ulva *Species***

The cosmopolitan genus *Ulva* Linnaeus, commonly known as the "sea lettuce," is represented by species distributed in all oceans and estuaries of the world, 17 of which have been recorded in the Mediterranean Sea (Guiry and Guiry 2008). Several species in this genus are commercially cultivated for human consumption in Asian countries or as a component in integrated multi-trophic aquaculture systems, e.g., for bioremediation of effluent and as a feed crop for abalone aquaculture in South Africa (Bolton et al. 2009). Furthermore, due to their higher biomass yield and the higher photosynthetic activity compared to the terrestrial crops, *Ulva* spp. are considered as a promising aquatic crop for biofuel production (Bruhn et al. 2011).

Some Ulva species are problematic to identify morphologically due to the extreme phenotypic plasticity in different environments (Hayden and Waaland 2004). Among them, *Ulva ohnoi* Hiraoka et Shimada, a green-tide-forming alga described from Japan, has been recently found in ballast water tanks of container ships in the Mediterranean Sea and may represent a newly introduced species in the basin (Flagella et al. 2010). *Ulva ohnoi* together with *Ulva prolifera* (Müller) J. Agardh were two of the species responsible for the world largest drifting macroalgal bloom in 2008 estimated as approx. one million tons of harvestable biomass (Qingdao, China, before the Olympic sailing competition; Leliaert et al. 2009; Pang et al. 2010).

Ulva species are well known for their broad environmental tolerance, high growth rate, and photosynthetic activity. They represent early successional, opportunistic species, often occurring in degraded or polluted (high nitrogen) environments, mainly due to their simple morphological features and the high reproductive success supported by the ability of gametes and zoospores to photosynthesize (Beach et al. 1995). Furthermore, *Ulva* species can survive up to 10 months in darkness and are therefore easily transported via ballast water tanks (Santelices et al. 2002).

12.4.7 Undaria pinnatifida

The brown seaweed *Undaria pinnatifida*, commonly known as “wakame,” is one of the most commonly eaten seaweeds in Japan. Large-scale commercial cultivation throughout Asia is primarily for human consumption; however, recently discovered antiviral compounds offer prospects for further commercial uses (Hemmingson et al. 2006). Invasive biological traits of *U. pinnatifida* are the very high growth rate (1–2 cm per day), high reproductive rate, long-range dispersal by floating reproductive thalli, the capacity for establishing populations in a variety of habitats and surfaces including artificial substrata, and the ability of gametophytes to colonize ship hulls (e.g., Casas et al. 2004; Thornber et al. 2004; Schaffelke et al. 2005; Russell et al. 2008). Due to the high biomass production and canopy-forming large blades, *U. pinnatifida* often outcompetes other algae by shading and space monopolization; however, ecosystem effects seem to vary greatly between introduced locations (reviewed in Schaffelke and Hewitt 2007).

12.4.8 Codium Fragile *Subspecies* Tomentosoides

Codium fragile (Suringar) Hariot sensu stricto is an edible green alga, widely consumed in Korea, China, and Japan. Cultivated in Korea, using seed stock produced from regeneration of isolated utricles and medullary filaments, the species is preferred to seaweeds such as *Porphyra* and *Undaria* because of its higher market value (Hwang et al. 2008). The protein and amino acid composition in this seaweed is similar to cereals like wheat, corn, and oats; its high content of minerals, dietary fiber, and low lipid content make the species a good candidate as a food additive in human and animal nutrition. In addition, bioactive compounds in *Codium fragile* ssp. *tomentosoides*, including anticancer agents and antibiotics are currently under investigation (Ortiz et al. 2009).

However, *Codium fragile* ssp. *tomentosoides* is one of the most invasive seaweeds, with significant ecological effects ranging from direct competition and replacement of native species to major changes at the community level (reviewed in Schaffelke and Hewitt 2007). In Chile, the invasive *Codium* strain competes with the native agarophyte *Gracilaria chilensis* causing potentially negative effects to the coastal economy by threatening the persistence of *G. chilensis* farms (Neill et al. 2006).

Several biological traits, related to life history and ecology of this ESU, are likely to be a reason for its invasive success. Invasive *Codium* benefits from both sexual and parthenogenetic proliferation as well vegetative propagation facilitated via thalli fragmentation and dispersal. Furthermore, colonization and the persistence of populations are facilitated by broad physiological tolerances to temperature and salinity regimes (Bégin and Scheibling 2003).

12.5 Conclusions

The relocation of marine species with invasive potential represents extraordinary challenges for marine ecosystems. In the future, the rate and range of introductions is likely to increase with increasing volume and speed of maritime traffic and with unprecedented changes in "recipient" environments by global climate change and local habitat degradation. Anticipating and controlling potential invasions is easier and more cost-effective than investing in posteriori management such as control and eradication efforts (e.g., Hewitt et al. 2009b).

The invasive seaweed species discussed in this chapter are recognized priority pest species with a high potential for negative ecological and socio-economic impacts (Doelle et al. 2007). However, where these seaweeds are native, many of them have long been exploited as valuable natural resources. The low capital costs of seaweed farming, good economic returns, and high demand for seaweed products in the world's market have led to intentional introductions of potentially invasive, high yield taxa like *Kappaphycus*, *Gracilaria*, and *Undaria* spp. and the expansion of farming areas, especially in developing and low-wage countries (Pickering et al. 2007). The incentives to introduce high-yield taxa are significant and the risks of intentional seaweed introductions have not yet been evaluated with cost-benefit analyses that include ecological and socio-economic consequences. The seaweed industry in the new millennium is predicted to grow with increasing demand for traditional seaweed products and for new applications of seaweeds, e.g., for the production of biofuels and bioactive compounds. Selective breeding and genetic modification to produce better cultivars for these applications is likely to add another dimension of uncertainty. New "super strains" with high invasive potential may be introduced to new locations with unprecedented consequences or may interbreed with con-specific native populations and increase their invasiveness.

The potential for controlled harvest has been suggested as a positive consequence of seaweed introductions, especially in areas where invasive seaweeds have established in high abundance and eradication or ongoing control is not economically feasible. However, stringent harvest regulations must be developed and applied to prevent further translocation and spread of invasive seaweeds into areas previously unaffected (see Schaffelke and Hewitt 2007).

In application of the precautionary principle of environmental management, preference should be given to the development of sustainable commercial seaweed culture in regions where a species (sensu stricto) occurs naturally. Valuable marine cultivars could be certified similar to D.O.P (protected denomination of origin) and D.O.C (controlled origin denomination) standards of agricultural crops, which would confirm that a seaweed has been produced in a specific geographical location. In addition, marine stewardship certifications would attest that a product is produced under certain environmental management and product quality standards. However, for this to happen seaweed products must attain a much higher commercial value than they currently have. In the meantime, a number of international agreements and voluntary codes of practice have been formulated to encourage national governments to restrict and control the intentional import and use of NIMS in aquaculture (reviewed in Hewitt et al. 2006). Also, recommendations for the assessment of proposals for intentional introductions are available to assist industries and regulators, even though quantitative data on ecological and socio-economic impacts of seaweed introductions are scarce. Research describing and assessing past and present NIMS invasions is vital to better predict future invaders, invaded regions, and the associated impacts and to support management and conservation decisions. At present, many questions around seaweed invasions and marine invasions, in general, remain to be answered (see e.g., Johnson 2007).

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Part III

Structure and Function of the World's Main Seaweed Systems

Chapter 13
Seaweeds and Their Communities in Polar Regions

Christian Wiencke and Charles D. Amsler

13.1 Introduction

The natural environment of polar seaweeds is characterized by strong seasonal light conditions and constant low temperatures (Zacher et al. 2011). At the northern and southern distribution limits of seaweeds in the Arctic (80°N) and Antarctic (77°S), the polar night lasts for about 4 months. At lower latitudes, e.g., the northern border of the Antarctic region, at King George Island (South Shetland Islands; 62°S) daylength varies between 20 h in summer and 5 h in winter. Sea-ice cover extends the period of hibernal darkness. If the ice is covered by snow under-ice irradiance can be reduced to $<2\%$ of the surface value. Extremely low irradiances ≤ 6.5 µmol photons m^{-2} s^{-1} have been measured even in midsummer (June) below a sea-ice cover and a snow layer of 30 cm in June on Arctic Spitsbergen (Hanelt et al. 2001). So, seaweeds can be exposed for long periods to darkness and very low light conditions. However, when the sea-ice breaks up solar radiation can penetrate deeply into the relatively clear water. In October/November 1993, average midday irradiances as high as 70 µmol photons m^{-2} s^{-1} were measured in 30 m water depth at King George Island (Gómez et al. 1997). At Signy Island (South Orkney Islands), the mean 1% depth of surface photosynthetically active radiation (PAR) is at about 29 m (Brouwer 1996a). Ultraviolet (UV) radiation as well can go down to considerable depths. In coastal areas, the 10% level for UV-A/UV-B radiation can be as deep as 7.1/4.3 m water depth, respectively, in summer (Richter et al. 2008).

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These relatively high light conditions prevail until phytoplankton blooms are formed and turbid melt-water carrying fine sediments and detritus flows into the sea (Drew and Hastings 1992). Thus, favorable light conditions for algal growth are present for only 2–3 months per year.

In contrast to the strong seasonality of the light conditions, seawater temperatures in the sublittoral vary only slightly between −1.8°C in winter and 2.2°C in summer in the Antarctic Peninsula region (Drew and Hastings 1992). At the boundary of the temperate region, maximum temperatures can reach 5°C in the Antarctic and 8–10°C in the Arctic (Wiencke et al. 2007). Temperature variation is, however, stronger in eulittoral and supralittoral communities. On King George Island, temperatures can go up to 14°C in tide pools while seaweeds exposed to air in the supralittoral experience temperatures up to nearly 30°C in summer and down to −27°C in winter (Zacher et al. 2011).

Although the current water temperatures in both polar regions are similar, the Arctic Oceans differ considerably in their cold-water history and their genesis. Whereas the water temperatures in the Southern Ocean have been low for 14 million years, glaciation and a winter sea-ice cover did not develop earlier than two million years in the Arctic (Crame 1993; Zachos et al. 2001; Zacher et al. 2011). Other differences between both polar regions refer to the connection with the temperate regions and to the nutrient levels in the seawater. Whereas the Antarctic region is strongly isolated, the Arctic region is continuously connected to temperate coasts. With respect to the nutrients, levels of nitrate and phosphate are high throughout the year in the Southern Ocean (Drew and Hastings 1992; Ducklow et al. 2007), while there is a strong seasonal variation of these levels in the Arctic. Here, nutrient levels are usually high during winter only and drop suddenly after sea-ice breakup (Chapman and Lindley 1980; Aguilera et al. 2002).

Seaweeds growing in such an extreme environment have to be adapted to these conditions. Their seasonal development must be tuned to the strong seasonality of the light conditions. Species from the Arctic must furthermore be adapted to the seasonal changes of the nutrient concentrations. An important prerequisite for seaweeds from polar waters is their capability to utilize the—for most parts of the year—prevailing low light conditions and, on the other hand, to sustain and use as efficient as possible the high light conditions during spring for photosynthesis.

The difference in the cold-water history of both polar regions has forced seaweeds in the Antarctic to reduce their temperature demands considerably compared to species from the Arctic (Gómez et al. 2011). Moreover, in conjunction with the strong geographic isolation of the Antarctic region, this has had great effects on biodiversity: Whereas in the Arctic only few endemic species occur, endemism is high in the Southern Ocean (Wulff et al. 2011). These environmental forcings influenced also the biotic interactions between seaweeds and their associated organisms. As we will discuss below, all these factors are important determinants of the functioning of polar seaweed communities.

13.2 Biodiversity and Biogeographical Relationships of Antarctic and Arctic Seaweeds

As mentioned above, both polar regions differ considerably with respect to their genesis and cold-water history. Antarctica is an ice-covered continent surrounded by the Southern Ocean without any land connection to temperate regions since the Mesozoic (Lawver et al. 1985). The Antarctic Circumpolar Current (ACC), which started to develop at about 32 Ma and became persistent around 15 Ma, amplifies this separation further (Hommersand et al. 2011). Driven by westerly winds, it flows clockwise around the continent. In contrast, the Arctic Ocean is a “mediterranean” sea surrounded by continental land masses and is continuously connected to the temperate coasts of Eurasia and America. The Arctic Polar Front is discontinuous and there is a strong influx of warm North Atlantic water into the Arctic through the Fram Strait between Spitsbergen and Greenland (Zacher et al. 2011). In contrast, the Antarctic region is sharply delimited to the north by the forceful Antarctic Polar Front. A second feature differentiating the two polar regions is their cold-water history. Whereas Antarctica became glaciated 14 million years ago (Crame 1993), a perennial ice cover over the Arctic Ocean did not develop before 0.7–2.0 Ma (Clarke 1990). So, seawater temperatures have been low for a much longer time in the Antarctic compared to the Arctic (Zacher et al. 2011).

These differences have resulted in strongly different biodiversity patterns in both polar regions. In the Antarctic region, 35% of the species are endemic, whereas only few endemic Arctic species have been identified so far (Wiencke and Clayton 2002; Wulff et al. 2011). In the Antarctic, 44% of the Heterokontophyta (Phaeophyceae and Chrysophyceae), 36% of the Rhodophyta, and 18% of the Chlorophyta are endemic and the number of endemic species is continuously increasing. Only recently, Hommersand et al. (2011) described four new genera and five new endemic red algal species. There is also one endemic order, the brown algal order Ascoseirales. Conspicuous and ecologically important endemic species include the brown algae *Himantothallus grandifolius*, *Desmarestia anceps*, *D. menziesii*, *Cystosphaera jacquinotii*, *Ascoseira mirabilis*, and the red algae *Myriogramme manginii*, *Georgiella confluens*, *Phycodrys antarctica*, *Trematocarpus antarcticus*, and others. The red algae *Palmaria decipiens* and *Iridaea cordata* occur from the Ross Sea in the south to a few sub-Antarctic islands in the north (Wiencke and Clayton 2002).

In contrast to the high degree of endemism in Antarctica, only very few seaweed species endemic to the Arctic have been detected (Wilce 1990; Wilce et al. 2009). These include the brown algae *Chukchia pedicellata*, *C. endophytica*, *Punctaria glacialis*, *Platysiphon verticillatus*, the red alga *Petrocelis polygyna*, and the green alga *Acrosiphonia incurva*. Most species from the Arctic have a distribution that extends well into the temperate region, e.g., the red algae *Devaleraea ramentacea*, *Turnerella pennyi*, *Dilsea integra*, and *Pantoneura baerii*. This is also the case for the kelp *Laminaria solidungula*, but this species is regarded as a true Arctic species as its occurrence in the temperate region is restricted to cold, deep waters (Müller et al. 2011).

A general characteristic of the floras of both polar regions is their low species richness. In the Antarctic, about 130 species have been documented (Wulff et al. 2011) and in the Arctic about 150 species have been recorded (Wilce 1994). These numbers will likely increase with increased exploration of these remote areas of our planet. In Antarctica, species richness is highest in the Antarctic Peninsula region and lowest in the southernmost part of the Ross Sea at 77°S (Wiencke and Clayton 2002). In the Arctic, species richness peaks with about 70 species around Svalbard, followed by the Canadian High Arctic (mainly Baffin Bay area) with 55 species. The Russian Arctic principally harbors an impoverished Svalbard flora. Similarly, species richness decreases in eastern Greenland from the south to the north. Whereas the seaweed flora in southernmost Greenland is relatively rich (Pedersen 1976), in the Alaskan Beaufort Sea shelf west of the Canadian Arctic Archipelago only 15 species were recorded (Dunton and Schonberg 2000; Wulff et al. 2011).

Two other characteristics of the Antarctic seaweed flora must be mentioned here: First, a conspicuous feature of the Antarctic seaweed flora, compared to temperate regions, is the scarcity of small macroalgal epiphytes. Such epiphytes are, however, not absent. Rather, they occur as endophytes in larger seaweeds (Peters 2003; see also Chap. 11 by Potin and Chap. 9 by Amsler). Second, the order Desmarestiales, which ecologically replaces the Laminariales (kelps) in Antarctica, is considered to have its evolutionary center in the Southern Ocean and subsequently radiated into the Northern hemisphere (Peters et al. 1997).

In contrast to the earlier assumption that Arctic seaweeds are mostly of Atlantic origin (Wilce 1990; Dunton 1992), recent molecular data obtained on six red algal species and of *Laminaria solidungula* from the Arctic indicate that Arctic and Atlantic subarctic species are evolutionary based in the North Pacific (Adey et al. 2008). Another example of an Arctic invader from the Pacific may be the green alga *Acrosiphonia arcta* (van Oppen et al. 1994). The species is—as is also *Desmarestia viridis*/*confervoides*—a good example for the evolution and spread of bipolar distributed species. According to molecular studies, the biogeographic disjunctions of both species date back to the maximum of the Würm/Wisconsin glaciation 18,000 years ago (van Oppen et al. 1993). The dispersal phases were presumably microscopic stages which, due to a high temperature tolerance, were able to cross the tropics (Peters and Breeman 1993; Bischoff and Wiencke 1995; see also Chap. 18 by Bartsch et al.).

13.3 Physiological Adaptations to the Environment

13.3.1 Seasonal Development and Physiological Performance

In polar regions, adaptation to the strong seasonality of the light regime is one of the most important prerequisites for the ecological success of seaweeds (Wiencke et al. 2011). There are two different growth strategies classified as season anticipators and season responders *sensu* Kain (1989). The season anticipators begin growing under short-day conditions in late winter/spring, often under the sea-ice. Some species even reproduce in winter. Maximal growth rates occur in spring. Growth and reproduction in these species are presumably based on circannual rhythms and photoperiodism, synchronized or triggered by daylength, as shown for some Antarctic (Wiencke 1990a; Wiencke et al. 1996) and for many cold-temperate species (Lüning 1988, 1991; Lüning and Kadel 1993; Schaffelke and Lüning 1994). The season responders, in contrast, start growth and reproduction later, not before favorable light conditions are present in spring and summer. Species of this group react directly to the primary factors in their environment and show an opportunistic life strategy (Wiencke 1990a).

Typical Antarctic season anticipators are the brown algae *Desmarestia menziesii, D. anceps*, *D. antarctica*, *Himantothallus grandifolius*, *Ascoseira mirabilis* (Wiencke 1990a; Drew and Hastings 1992; Gómez et al. 1995, 1996; Gómez and Wiencke 1997) and the red algae *Palmaria decipiens*, *Delesseria salicifolia*, *Gymnogongrus antarcticus*, *G. turquetii*, *Hymenocladiopsis crustigena*, *Trematocarpus antarcticus*, and *Phyllophora ahnfeltioides* (Wiencke 1990b; Weykam et al. 1997; Dummermuth and Wiencke 2003). Typical Antarctic season responders are *Adenocystis utricularis* (Wiencke 1990a), the red algae *Iridaea cordata* (Weykam et al 1997) and *Gigartina skottsbergii* (Wiencke 1990b), and the green algae *Ulva hookeriana* and *Acrosiphonia arcta* (Wiencke 1990b).

In contrast to the Southern Ocean in the Arctic there is not only a strong seasonal variation of the light regime, but also of the levels of the macronutrients nitrate and phosphate, which are high in winter and low in summer (see Chap. 4 by Gordillo). Arctic season anticipators like *Laminaria solidungula* and *Saccharina latissima* (*L. saccharina*) take full advantage of these conditions (Chapman and Lindley 1980; Dunton 1985). New blades start to form in *L. solidungula* in fall under decreasing daylengths. Optimum growth rates occur in late winter/spring under thick ice. In comparison, *S. latissima* grows mostly during a brief period in late spring, when the first light penetrates into the water during sea-ice breakup.

As most endemic Antarctic and Arctic seaweeds are season anticipators, this type of life strategy is therefore regarded as the typical adaptation to the seasonally changing conditions in polar seas. In contrast, season responders are mostly distributed also in the adjacent temperate regions. Another difference between both groups is their depth distribution. Polar season anticipators occur almost exclusively in the sublittoral, whereas many polar season responders can grow also in the eulittoral.

As for biomass formation, photosynthetic performance shows also a strong seasonal pattern (Wiencke et al. 2011). In large brown algal season anticipators, photosynthetic rates are highest in late winter/spring (Drew and Hastings 1992; Gómez et al. 1995). As shown in several kelp and kelp-like species, respiration rates increase indicating growth activity in the basal meristem powered by remobilization of carbohydrates from the distal thallus part. An extreme example is *Laminaria solidungula*, in which the mobilization occurs during the 9 months period of darkness under the ice, when the alga completes over 90% of its annual growth.

During this time, up to 30% of its original total carbon content is depleted before photosynthetic production begins in spring. During summer, high photosynthetic rates are used for carbon storage and not for biomass formation (Dunton and Schell 1986; see also Chap. 2 by Gómez and Huovinen).

In the Antarctic red algal season anticipator *Palmaria decipiens*, photosynthetic rates are—like the growth rates—highest in spring. There is a positive correlation between the phycobilin content, photosynthetic capacity and efficiency, which are highest in fall, winter, and spring. During summer, the alga reduces the photosynthetic apparatus to a minimum (Lüder et al. 2001a). The presence of two phycobilisome forms with different aggregation states has been regarded as special advantage for a rapid acclimation to changing environmental light conditions (Lüder et al. 2001b; see also Chap. 1 by Hanelt and Figueroa).

The effect of darkness on physiological performance has been studied in *Palmaria decipiens* and *Iridaea cordata*. In *P. decipiens*, the light harvesting phycobilisomes and later, the chl *a* containing inner antennae are degraded during long-term exposure to darkness. After 6 months, the alga has lost its ability to photosynthesize. Following reexposure to light, pigments are rapidly synthesized and after a week photosynthesis recovers to normal levels (Lüder et al. 2002; Weykam et al. 1997). In contrast, the season responder *I. cordata* maintains a functional photosynthetic apparatus during dark-exposure and is therefore better suited to grow in places with less predictable light conditions (Weykam et al. 1997; see also Chap. 1 by Hanelt and Figueroa).

Overall, seasonal development and physiological performance exhibit many similarities with temperate seaweeds. Although there is no unique mechanism occurring only in polar species, their efficient adaptations to low light, however, allow Arctic and Antarctic species to thrive with great success in polar waters.

13.3.2 Radiation Climate and Depth Zonation

In polar regions, the radiation climate imposes severe constraints not only with respect to seasonal light availability but also with respect to the irradiance level in different water depths ultimately determining seaweed zonation. As polar algae are mainly sublittoral, low light tolerance is a prerequisite for distribution down to great depths. This becomes obvious when the minimum light requirement for completion of the life history is considered, which is lower in polar seaweeds compared to temperate, morphologically similar species. For Antarctic Desmarestiales, the minimum annual light demand is 31 moles photons m^{-2} (Wiencke 1990a) and for *Laminaria solidungula* 45–49 moles m^{-2} (Chapman and Lindley 1980; Dunton 1990). In contrast, *L. hyperborea* from the North Sea requires 71 moles m^{-2} per year (Lüning and Dring 1979).

Another prerequisite for algal life in polar waters is a capacity to tolerate long periods of darkness. Various polar seaweeds tolerate darkness for up to 18 months (tom Dieck 1993; Wiencke 1990a). Growth in the microscopic stages of Antarctic seaweeds is light-saturated at photon fluence rates as low as 4–12 μmol photons m^{-2} s^{-1} (Wiencke 1990a). In young sporophytes of Antarctic Desmarestiales the values are somewhat higher, at 15–20 μmol photons m^{-2} s^{-1} (Wiencke and Fischer 1990).

As with growth, the light demands for photosynthesis are also very low. Species from both polar regions show a high photosynthetic efficiency (α), low respiratory rates, low saturation points for photosynthesis (E_k), and low compensation points for photosynthesis (E_c; Gómez et al. 2011). E_k values range between 3 and 100 μmol photons m^{-2} s^{-1}, and E_c values between <1 and 15 μmol photons m^{-2} s^{-1}, values usually lower than for species from temperate regions (Lüning 1990).

Generally, E_k values for photosynthesis are higher than the irradiances required for saturation of growth. This represents an important ecological advantage for coping with the strong fluctuations of incident irradiance during the open water period. While growth is saturated at low irradiances, the photon fluence rates above the saturation point for growth can be used for purposes other than growth, e.g., for formation of storage compounds. For example, Antarctic seaweeds growing at depths below 20 m are often exposed to irradiances around 80 μmol photons m^{-2} s^{-1} during late winter/spring (Gómez et al. 1997) allowing considerable carbon fixation, fuelling—aside from growth—other metabolic processes.

The light requirements for photosynthesis are an important factor for the determination of zonation patterns. If one relates the daily light course of the irradiance to the E_k value, it is possible to estimate the average daily period of light saturation, called H_{sat}. The obtained metabolic daily carbon balance is regarded as a physiological indicator for the ability to live in deep waters. *Laminaria solidungula* in the Alaskan Beaufort Sea at 70°N was for example exposed in 1986 to total H_{sat} periods of 148 h (Dunton 1990), corresponding to an average daily H_{sat} of 3 h. For five red and brown algae from King George Island (Antarctica), H_{sat} determined during the clear water period in spring decreases with depth from values close to 14 h at 10 m to values between 7 and 12 h at 30 m depths (Gómez et al. 1997). For the red algal species *Palmaria decipiens*, *Trematocarpus antarcticus*, and *Gigartina skottsbergii* the carbon balance was between 1.7 and 2.5 mg C g FW $^{-1}$ d^{-1} at 10 m depth and between 0.6 and 0.8 mg C g FW $^{-1}$ d^{-1} at 30 m depths, setting the lower depth limit at >30 m. For the kelp-like brown alga *Himantothallus grandifolius*, the daily carbon balance varied between 0.6 and 1.0 mg C g FW $^{-1}$ d^{-1} over the studied range of 10–30 m, indicating that this species can potentially occur even deeper, which is actually the case. In contrast, in the brown alga *Desmarestia anceps* the negative (!) carbon balance of -1.9 mg C gFW^{-1} d^{-1} limits the alga to depths of about 30 m at this location (Gómez et al. 1997). Based on photosynthetic measurements, the lower depth distribution limit of the red alga *Myriogramme manginii* at Signy Island (South Orkney Islands) has been predicted to be at approx. 23 m water depth (Brouwer 1996a).

Polar seaweeds are not only strongly shade-adapted but can also cope with high light conditions in summer because of their ability for dynamic photoinhibition, a photoprotective mechanism, by which excessive energy absorbed is rendered harmless by thermal dissipation (see Chap. 1 by Hanelt and Figueroa).

Deep water species are strongly photoinhibited when exposed to high light conditions and recover during subsequent exposure to favorable light only slightly and slowly (Hanelt 1998; Karsten et al. 2001), whereas in eulittoral and upper sublittoral species the decrease in photosynthetic activity is less pronounced and usually a strong and quick recovery is recorded.

Similarly, UV radiation is also regarded as key factor affecting the depth zonation of seaweeds (Karsten et al. 2011). As explained in Chap. 20 by Bischof and Steinhoff, UV-B radiation has damaging effects on various cellular structures and processes, among those on the DNA and photosynthesis. However, damage can be repaired and there are also protective mechanisms to prevent damage. The result can be impaired growth or impaired reproductive capacity. The life-history stages of seaweeds most susceptible to UV radiation are spores. Field experiments have clearly shown that the upper depth distribution limit of Arctic kelps is determined by the UV susceptibility of their spores (Wiencke et al. 2006). Consequently, the succession of polar seaweed communities also depends on the UV radiation regime as explained below. Certainly, metabolic carbon balance and UV radiation are not the only factor controlling the lower and upper depth distribution limits. Substrate, ice abrasion, and competition play besides other factors important roles.

13.3.3 Temperature Requirements and Geographic Distribution

Polar seaweeds are well adapted to the low seawater temperatures, and Antarctic seaweeds more strongly than Arctic species due to the longer cold-water history of the Southern Ocean (see Chap. 18 by Bartsch et al.). Sporophytes of endemic Antarctic Desmarestiales, for example, grow up to 5°C and exhibit upper survival temperatures (USTs) of 11–13°C. Their gametophytes grow up to 10 or 15°C with USTs between 15 and 18°C (Wiencke et al. 1994). The Antarctic red algae *Georgiella confluens*, *Gigartina skottsbergii*, and *Plocamium cartilagineum* grow at 0°C, but not at 5°C and have USTs as low as 7–11°C (Bischoff-Bäsmann and Wiencke 1996). Antarctic cold-temperate species, especially from the eulittoral, are characterized by higher temperature ranges (Wiencke et al. 1994; Gómez et al. 2011).

In contrast, sporophytes of the endemic Arctic kelp *Laminaria solidungula* grow up to temperatures of 15°C with optimum growth rates at 5–10°C and an UST of 16°C. The gametophytes of this species exhibit an UST of 20°C (Bolton and Lüning 1983; tom Dieck 1992). No data are available on the temperature demands of other endemic Arctic species. The Arctic cold-temperate red alga *Devaleraea ramentacea* grows at temperatures up to 10°C and exhibits USTs of 18–20°C (Novaczek et al. 1990; Bischoff and Wiencke 1993). Clearly, more data are needed also on the temperature dependence of other processes in the life history.

The strong adaptation of Antarctic seaweeds to low temperatures is also reflected in their photosynthetic performance. Maximum photosynthetic rates of endemic Antarctic species are at 0°C in a similar range compared to temperate species measured at higher temperatures. Moreover, the temperature optima for photosynthesis in the few tested Antarctic species are well below values determined in temperate species (Gómez et al. 2011). Likewise, the optimum temperature for photosynthesis in zoospores of *Alaria esculenta*, *Laminaria digitata*, and *Saccharina latissima* from Arctic Spitsbergen is with 7–13°C relatively low (Roleda 2009). In contrast, the optima for respiration are clearly located at higher temperatures. Photosynthesis:respiration (P:R) ratios in Antarctic species are highest at the lowest tested temperature (0°C) and decrease with increasing temperatures due to different Q_{10} values for photosynthesis (1.4–3.5) and respiration (2.5–5.1; Gómez et al. 2011). The high P:R ratios at low temperatures explain the high growth rates of polar species at low temperatures, which in the end determine the geographic distribution.

The northern distribution of endemic Antarctic species is often limited by the temperature demands for growth. Endemic Antarctic Desmarestiales for example occur only south of the Antarctic Polar Front in areas with maximum temperatures $\leq$5°C allowing sufficient growth of their sporophytes (Wiencke et al. 1994; Müller et al. 2011; see also Chap. 18 by Bartsch et al.). The southern distribution of Arctic-North Atlantic species is often limited both by the USTs and the upper limit of gametogenesis (van den Hoek 1982a, b). In the West Atlantic distribution limits are determined by lethal, high summer temperatures, whereas in the East Atlantic they are determined by high winter temperatures inhibiting reproduction. Examples for species from this group are *Laminaria digitata*, *Chorda filum*, and *Halosiphon tomentosus*.

During the ice ages, both the Arctic and the Antarctic were not hospitable for seaweeds. In the southern hemisphere, sub-Antarctic islands and the southern tip of South America have probably served as refugia. Migration of species from Antarctica to South America and vice versa probably took place along the Scotia Arc (Wiencke et al. 1994). In the northern hemisphere, the distribution area of Atlantic seaweeds was extremely reduced during the ice ages. In the north, their distribution was limited by the glaciers and in the south by the 10–15°C winter isotherm, their southern reproduction boundary. This most probably explains the present depauperate flora in the North West Atlantic. A comparable situation did not exist in the Pacific, probably a major reason for the richness of the cold North Pacific (Wiencke et al. 1994). The temperature decrease during the ice ages allowed polar species to extend their distribution limits toward the equator. Some species even crossed the equator during the maximum of the last glaciations (see Chap. 18 by Bartsch et al.; Wiencke et al. 1994).

13.3.4 Effect of Salinity, Temperature, and Desiccation on Supra- and Eulittoral Seaweeds

Information on osmotic acclimation of supra- and eulittoral seaweeds during salinity changes is available only for green algae from the Antarctic. Eulittoral species survive salinities between 7 and 102 psu and grow between 7 and 68 psu.

The supralittoral species *Prasiola crispa* has even a broader growth range between 0.3 and 105 psu (Karsten et al. 1991a, b; Jacob et al. 1991). The general mechanisms of osmotic acclimation are the same as also in species from other regions (Kirst 1990; Wiencke et al. 2007; see Chap. 5 by Karsten). Major inorganic osmolytes are potassium, sodium, and chloride. These osmolytes are used during short-term osmotic regulation. Long-term osmotic stress is counterbalanced by various compatible organic solutes, among them β-dimethylsulphoniumproprionate (DMSP), the imino acid proline, and sucrose (Karsten et al. 1991b; Jacob et al. 1991).

Decreasing temperatures also strongly stimulate the biosynthesis and accumulation of DMSP in Antarctic green algae stabilizing the structure of the enzymes lactate dehydrogenase and malate dehydrogenase of *Acrosiphonia arcta* (Karsten et al. 1996). Ice-binding proteins (IBP) that modify the shape of growing intracellular ice crystals during freezing were recently detected in Antarctic *Prasiola* and sea-ice diatoms (Raymond and Fritsen 2001). Presumably, IBPs prevent damage to membranes by the inhibition of the recrystallization of ice (Raymond and Knight 2003).

The low temperatures in the eulittoral and supralittoral represent a challenge to algal physiology because they are often combined with high irradiances in summer. At low temperatures enzyme activities and turnover velocity of the D1 reaction center protein in photosystem II are reduced (Andersson et al. 1992; Aro et al. 1993), which may result in increased electron pressure in photosynthesis and ultimately in the generation of reactive oxygen species (Dring 2006). The consequences of increased oxidative stress are chronic photoinhibition/photoinactivation, bleaching of photosynthetic pigments, peroxidation of membrane lipids, and enhanced degradation of D1 protein (see Chap. 6 by Bischof and Rautenberger). Eulittoral species, such as the green algae *Urospora penicilliformis* and *Ulva hookeriana*, the red alga *Porphyra endiviifolia*, and the brown alga *Adenocystis utricularis* may overcome radiation stress at low temperatures by their ability for dynamic photoinhibition/photoprotection, which proceeds much faster than in sublittoral algae (Hanelt et al. 1994, 1997). In the upper sublittoral red alga *Palmaria decipiens*, for example, there was a persistent impairment of photosynthetic activity at 0°C combined with irradiances of 400 µmol photons m^{-2} s^{-1}, but not at 200 µmol photons m^{-2} s^{-1}. In contrast, photosynthesis was not impaired under both light intensities at 8°C (Becker et al. 2011).

The effects of freezing in combination with high light intensities on photosynthesis were studied in the Arctic eulitttoral brown alga *Fucus distichus*. There was a marked decrease of optimum quantum yield with decreasing temperatures down to −10/−15°C and a rapid recovery as soon as the temperatures increased again (Becker et al. 2011). While photosynthetic activity was zero at 15°C in this species, in the Antarctic green alga *Prasiola* photosynthetic activity was observed down to −15°C (Becker 1982). The physiological basis of this extraordinary capacity is not known.

Desiccation is a strong stress parameter in supralittoral species (see also Chap. 5 by Karsten). Thalli of *Prasiola crispa* lose 75% of the cellular water during the first 6 h of exposure to air (Jacob et al. 1992). Irreversible damage occurred after a water loss of more than 90%. Growth rates after reimmersion in seawater depend on the thallus water content and the length of the desiccation period. Few ultrastructural changes were found after desiccation, but the very thick cell walls of the species and the absence of vacuoles are regarded as prerequisites for surviving periods of desiccation (Jacob et al. 1992).

13.4 Ecology of Polar Seaweed Communities

13.4.1 Biomass, Depth Distribution, and Productivity

As a result of the harsh environmental conditions, most seaweeds of the polar regions occur almost entirely in the sublittoral. In Antarctica, seaweeds dominate shallow benthic communities on hard substrates along the northern portion of the western Antarctic Peninsula and adjacent islands, often covering over 80% of the bottom with standing biomass levels in the range of 5–10 wet kg m^{-2}, which is comparable to temperate kelp forests (Amsler et al. 1995; Brouwer et al. 1995; Quartino et al. 2001; Quartino and Boraso de Zaixso 2008). Low intertidal pools and crevices in the upper sublittoral are frequently colonized by the red algae *Iridaea cordata* and *Palmaria decipiens*. Below this zone several species of large, perennial brown algae are particularly abundant. *Desmarestia menziesii* (shallower) and/or *D. anceps* (deeper) typically dominate in waters from 2 to 3 m down to approximately 10–20 m with *D. anceps* sometimes the dominant species to 30 m or more. *Himantothallus grandifolius* typically dominates from whatever depth at which the *Desmarestia* spp. thin out down to 40 m or greater (DeLaca and Lipps 1976; Zielinski 1990; Klöser et al. 1994; Amsler et al. 1995; Brouwer et al. 1995; Quartino et al. 2001) with productivity estimates in the northern part of its range estimated as 16–56 g C m^{-2} $year^{-1}$ (Drew and Hastings 1992). *Cystosphaera jacquinotii* often co-dominates with *H. grandifolius* or *D. anceps* below 20 m in relatively wave-exposed areas (Zielinski 1990; Chung et al. 1994; Amsler personal observations). These brown algal stands are accompanied by various undergrowth species, besides the mentioned *P. decipiens* and *I. cordata*, the red algae *Gigartina skottsbergii, Myriogramme manginii*, *M. smithii*, *Trematocarpus antarcticus*, *Gymnogongrus turquetii*, *Georgiella confluens*, and others (Wiencke and Clayton 2002; Wulff et al. 2011). In total, over 100 species of seaweeds are found in shallow water along the Antarctic Peninsula (Moe and DeLaca 1976; Klöser et al. 1996; Wiencke and Clayton 2002).

This general pattern of seaweed dominance is reported from numerous locations along the western Antarctic Peninsula region from its northeastern limit at Signy Island (60°S latitude) south to Anvers Island (64°S; e.g., Neushul 1965; Delépine et al. 1966; DeLaca and Lipps 1976; Lamb and Zimmerman 1977; Rakusa-Suszczewski and Zielinski 1993; Amsler et al. 1995; Brouwer et al. 1995; Klöser et al. 1996; Quartino et al. 2001). However, the limited reports of seaweed abundance and distribution on the southern half of the western Antarctic Peninsula describe a drop off in both species richness and biomass as one moves south from Anvers Island (DeLaca and Lipps 1976; Moe and DeLaca 1976; Barnes and Brockington 2003; Bowden 2005). Moe and DeLaca (1976) hypothesized that the decreases in biomass and diversity in more southerly sites are largely due to increases in annual ice cover. This relative decrease in biomass and coverage is not unique to the southern Antarctic Peninsula since the same qualitative patterns are described at other locations of similar latitude throughout most of the coast of Antarctica (e.g., Zaneveld 1966; Dhargalkar et al. 1988; Kirkwood and Burton 1988; Johnston et al. 2007). However, even at these locations seaweeds can dominate their communities. For example in East Antarctica, Irving et al. (2005) reported that *Himantothallus grandifolius* covered approximately 80% of the bottom at 12 m depth at two sites with the red seaweed, *Palmaria decipiens*, covering nearly all the remaining substrate and in another area Johnston et al. (2007) reported 80–90% cover of *Desmarestia* sp. and *P. decipiens* at 6 m depth and approximately 80% cover of *H. grandifolius* at 12 m.

In the southern-most Antarctic seaweed habitats in the Ross Sea, communities dominated by the frondose red seaweeds *Iridaea cordata* and *Phyllophora antarctica* and the crustose coralline alga *Phymatolithon foecundum* have been studied at Terra Nova Bay (74°, 40′ S; reviewed by Cattaneo-Vietti et al. 2000; Cormaci et al. 2000) and in McMurdo Sound (77° 40–50′ S Miller and Pearse 1991). *I. cordata* is more abundant in the 2–10 m depth range with densities up to 4,000 individuals m^{-2} and wet biomass levels up to 3.5 kg m^{-2} (Cattaneo-Vietti et al. 2000). *P. antarctica* dominates from 10 to 20 m depth with densities up to 10,000 individuals m^{-2}, wet biomass levels up to 1.6 kg m^{-2}, and percent cover up to 90% of the benthos (Miller and Pearse 1991; Cattaneo-Vietti et al. 2000). *P. foecundum* includes several coralline alga species previously reported from the Ross Sea (Alongi et al. 2002) and occurs to depths of 70 m (Cormaci et al. 2000). In McMurdo Sound, it is present at most sites which have been observed by divers whereas the foliose red algae occur at only a minority of locations (Miller and Pearse 1991; Amsler, personal observations). Both *P. foecundum* (Miller and Pearse 1991) and *I. cordata* (R. Robbins, personal communication) occur at Cape Armitage in McMurdo Sound, which is the southern-most point in the world where open ocean occurs over waters shallow enough to support seaweeds.

In the Arctic, several studies have documented seaweed communities growing on boulders as well as smaller rock and shell hard substrates in the Alaskan Beaufort Sea. These communities are dominated by the kelp *Laminaria solidungula* along with lesser numbers of the kelps *Saccharina latissima* and *Alaria esculenta*, six species of foliose red seaweeds, and crustose coralline red algae (Dunton et al. 1982; Busdosh et al. 1983). Wet biomass values for the kelps range from means of 0.067 kg m^{-2} where only 10–25% of the bottom is covered by rock to 0.26 kg m^{-2} where rock covers >25% of the bottom (Dunton et al. 1982). Kelp densities are higher in summer than winter, with maximum densities of 6–30 individuals m^{-2} in patches with high percentages of rock (Busdosh et al. 1983). The total mean wet biomass of red seaweeds is approximately 0.12 kg m^{-2} (Dunton et al. 1982).

L. solidungula productivity in this system has been estimated as 6–10 g C m^{-2} year^{-1} (Dunton and Schell 1986) compared to an estimate of up to 20 g C m^{-2} year^{-1} in the Canadian High Arctic (Chapman and Lindley 1980). In this area, however, there are no intertidal algae and seaweeds are restricted to small areas on hard substrata protected from ice scour (Dunton and Schonberg 2000).

At another Arctic location, at Hansneset in the middle part of Kongsfjorden in Svalbard, seaweed communities are better developed and include a greater diversity of species. The intertidal zone supports *Fucus distichus* and smaller brown algae while the shallow subtidal down to 2.5 m is characterized by several annual or pseudo-perennial seaweeds (Hop et al. 2002; Wulff et al. 2011). Important species are the green algae *Acrosiphonia* spp., *Spongomorpha* spp., and the brown algae *Chordaria flagelliformis* and *Chorda filum* (Wulff et al. 2011). The zone between 5 and 15 m is dominated by kelps including *Saccorhiza dermatodea*, *Alaria esculenta, Laminaria digitata*, and *Saccharina latissima*, along with a diversity of smaller red, green, and brown seaweeds (Wiencke et al. 2004). Overall, over 70 seaweed species occur here with wet biomass values ranging from 0.02 to 21 kg m^{-2} (Hop et al. 2002). Below this zone of kelps and kelp-like species *Desmarestia aculeata* and *D. viridis* can be very frequent (Beuchel and Gulliksen 2008). At greater depths red algae dominate the community, in particular *Coccotylus truncatus* and *Phycodrys rubens*, the latter growing down to as deep as 60 m (Wiencke, unpublished data). The endemic Arctic *Laminaria solidungula* occurs in deep water in the inner (colder) part of Kongsfjorden or as undergrowth species in the kelp forest. The inner part of the fjord is characterized by high sedimentation rates (Svendsen et al. 2002) and consequently by a much lower biodiversity. The described zonation pattern is in principle also typical for the Russian Arctic coast, eastern Greenland, and the Canadian high Arctic (Wulff et al. 2011).

The few studies on succession in polar seaweed communities were recently summarized by Campana et al. (2011). Succession starts with rapid colonizers, e.g., diatoms and ephemeral seaweeds and goes on with a recruitment of annual and perennial seaweed species in late winter–spring. Colonization is severely affected by physical disturbance and seasonal changes in abiotic conditions including UV stress (see Chap. 20 by Bischof and Steinhoff; Karsten et al. 2011) as well as by biotic factors, such as grazing (Zacher et al. 2007).

13.4.2 Elemental and Nutritional Content

Compared to seaweeds in almost all other parts of the world, Antarctic seaweeds have relatively low Carbon to Nitrogen (C:N) elemental ratios and relatively high tissue nitrogen levels (Dhargalkar et al. 1987; Weykam et al. 1996; Dunton 2001; Peters et al. 2005). This indicates that they are unlikely to be growth limited by nitrogen, which is probably a result of the relatively high nitrogen and other nutrient levels present in Antarctic coastal waters throughout the year (Weykam et al. 1996;

Peters et al. 2005; see Chap. 4 by Gordillo). Not surprisingly then, protein levels in Antarctic macroalgae are also higher than reported for most other places in the world (Peters et al. 2005). Since protein levels are important determinants of the nutritional value and palatability of seaweeds to herbivores (e.g., Horn and Neighbors 1984), this suggests that were it not for the common occurrence of chemical defenses in these algae they would likely be more valuable foods for herbivores than seaweeds from other regions. In the only study we are aware of in the Arctic, *L. solidungula* and *S. latissima* were shown to also have relatively low C:N ratios early in the growing season which increased as stored nitrogen was used for biomass gain during the summer (Henley and Dunton 1995).

13.4.3 Defenses Against Herbivory and Biofouling in Polar Seaweeds

Many seaweeds deter herbivores with organic compounds that make them unpalatable and/or interfere with the animals' digestion, and similar compounds can also be used to deter the settlement of biofouling spores or larvae (see also Chap. 8 by Iken and Chap. 9 by Amsler). In addition or as an alternative to chemical defenses, seaweeds can also decrease their palatability to herbivores by increasing their physical toughness (e.g., Lowell et al. 1991).

Chemical defenses against herbivores are very common in Antarctic seaweeds (Amsler et al. 2005a, 2008, 2011; Aumack et al. 2010). All of the dominant brown seaweeds along the western Antarctic Peninsula described and most of the common red seaweeds in the subtidal community elaborate chemical defenses against herbivores. Although physical toughness may play a role in some species, particularly against amphipods, chemical defenses appear to be far more important overall in deterring herbivory (Amsler et al. 2005a, 2008, 2011). Hence, although these communities are similar to temperate kelp forests in being dominated by large, perennial brown seaweeds, they differ from many such communities in that the seaweeds are able to resist herbivory directly rather than relying on top-down control of herbivores by their predators (e.g., Elner and Vadas 1990; Estes and Duggins 1995).

Both of the dominant red seaweeds in the Ross Sea, *I. cordata* and *P. antarctica*, are also chemically defended against a sea urchin which is the most obvious potential algal consumer in that system (Amsler et al. 1998). However, the sea urchins preferentially cover themselves with detached seaweeds when they are available, which in turn provides a physical barrier for defense against their main predator, large sea anemones (Amsler et al. 1999). This benefits the seaweeds since it keeps a large population of drift algae in the photic zone where they continue to photosynthesize and reproduce (Amsler et al. 1999; Schwarz et al. 2003).

The palatability of 19 seaweeds to herbivorous sea urchins and amphipods has been examined in the Arctic at Svalbard (Wessels et al. 2006). Of these, 17 seaweed species were unpalatable. By comparing assays on fresh seaweed thallus with artificial foods which removed physical defenses, it was concluded that 15 of the 17 seaweeds rely primarily on physical toughness to deter herbivores and that only two elaborate chemical defenses (Wessels et al. 2006). In one of these chemically defended seaweeds, *Desmarestia viridis*, the defensive compound has been shown to be sulfuric acid (Molis et al. 2008). *D. viridis* provides associational defense to other seaweeds growing near because it so strongly repels sea urchins (Molis et al. 2008).

To date, no studies—we are aware of—have examined polar seaweed chemical defenses against biofouling in an ecologically relevant context (see also Chap. 9 by Amsler). However, Antarctic seaweeds do produce compounds which are toxic to epiphytic diatoms in vitro (Amsler et al. 2005b; Iken et al. 2011; Sevak 2010). Grazing amphipods appear to be very important in reducing diatom fouling of these seaweeds in nature (see also Chap. 8 by Iken). However, when held in experimental mesocosms without amphipods, one of four species, *Desmarestia anceps,* still had only very low diatom coverage even though the other three species were heavily fouled (Aumack et al. 2011). *D. anceps* is one of the many species which have anti-diatom bioactivity in vitro, and it is possible that some of these compounds are also playing a role in controlling fouling in nature.

13.4.4 Trophic Interactions

Antarctic seaweeds appear to play important roles in benthic food webs in both shallow and deeper waters along the northern portion of the Antarctic Peninsula and they are likely to be of particular importance to benthic detrital food chains. A majority of the mid-water and, in particular, deep water carbon flux along the western Antarctic Peninsula can be composed of seaweed material, which also forms a significant part of the sediments (Liebezeit and von Bodungen 1987; Reichardt 1987; Fischer and Wiencke 1992). Seaweeds are also important in Antarctic coastal and maritime detrital food chains along the western Antarctic Peninsula (Zielinski 1981; Dawson et al. 1985). Drift seaweeds can be abundant in pockets on the coastal sea floor (Neushul 1965; Brouwer 1996b; Amsler, personal observations). A major portion of the primary production of *Himantothallus grandifolius* is lost as blade erosion and, in contrast to phytoplankton, this carbon input to the detrital communities continues throughout the year (Dieckmann et al. 1985). Although living, drift *Desmarestia anceps* decays fairly slowly via fragmentation, carbon from dead *D. anceps* is recycled relatively quickly (Brouwer 1996b). Stable isotope techniques have shown that macroalgal carbon makes important contributions to invertebrates via the detrital food webs in both shallow hard bottom communities where they grow (Dunton 2001) and in nearby, soft bottom communities (Corbisier et al. 2004) along the western Antarctic Peninsula. In McMurdo Sound, *Phyllophora antarctica* appears to be a similar, important source of carbon to hard and soft bottom communities, likely via the detrital food web (Norkko et al. 2004).

Antarctic seaweeds also provide food and cover to large numbers of invertebrates and fishes (e.g., DeLaca and Lipps 1976; Richardson 1977; Iken 1999; Huang et al. 2007; Zamzow et al. 2011). Amphipods occur on these seaweeds at exceptionally high densities. Richardson (1977) reported over 10,000 amphipods per single *Desmarestia anceps* while Amsler et al. (2008), combining datasets from the same community collected by Amsler et al. (1995) and Huang et al. (2007), estimated densities of amphipods in solid stands of *D. menziesii* at over 300,000 individuals m^{-2} of the benthos with densities in solid stands of *D. anceps* and *Plocamium cartilagineum* of approximately 30,000 individuals m^{-2}. All the seaweed species that have been reported with very high amphipod densities are also chemically defended against amphipod herbivory (Amsler et al. 2005a; Huang et al. 2007; Aumack et al. 2010) and as such are almost certainly not being consumed by the amphipods. Instead, the amphipods are grazing epiphytic diatoms and other macroalgae, as well as filamentous algal epiphytes and emergent filaments from algal endophytes (Aumack et al. 2011). Removing these biofouling algae undoubtedly benefits the host seaweeds. The amphipods also benefit from associating with the chemically defended seaweeds as they are much less likely to be consumed by omnivorous fish (Zamzow et al. 2010). Therefore, the seaweeds, which are the dominant, habitat-forming organisms in the community and the amphipods, which are by far the most numerous animals in the community, exist in a community-wide, mutualistic relationship.

Filamentous algae growing as epiphytes are very rare along the western Antarctic Peninsula (Peters 2003). However, filamentous algae growing as endophytes within the larger, chemically defended seaweeds are unusually common, which has probably been selected for as a refuge from the dense amphipod assemblage (Peters 2003; Amsler et al. 2009; see also Chap. 9 by Amsler and Chap. 11 by Potin). Although endophytes do not necessarily harm their hosts, serious pathogenic effects of filamentous algal endophytes on their seaweed hosts are well known (e.g., Apt 1988; Correa and Sánchez 1996; Peters and Schaffelke 1996). Whether or not, and if so how frequently, the abundant algal endophytes in Antarctic seaweeds are deleterious to their hosts and whether or not Antarctic seaweeds use chemical defenses against endophytes are important areas for future study.

Although seaweeds in Arctic Spitsbergen support a diversity of macrofauna (Lippert et al. 2001; Włodarska-Kowalczuk et al. 2009), only 2 of 19 such species examined were shown to consume the seaweeds (Wessels et al. 2006). However, it is likely that, as in Antarctica, seaweed carbon is important in this system via the detrital food web (Hop et al. 2002). In the Alaskan Beaufort Sea, stable isotope techniques have shown that kelps are an important carbon source to many invertebrate species including direct herbivores and animals deriving the carbon via detritus (Dunton and Schell 1987).

13.5 Impact of Global Climate Changes on Seaweeds and Their Communities

As stratospheric ozone depletion is highest in polar regions, numerous studies were performed on the effect of enhanced UV radiation (UVR) on seaweeds from the Arctic and Antarctic (see Chap. 20 by Bischof and Steinhoff; Karsten et al. 2011). The most UV-susceptible stages in the life history of seaweeds are their spores (Roleda et al. 2007). Spores of shallow water species exhibit a high UV tolerance, whereas spores of mid- and lower sublittoral species are increasingly UV susceptible (Wiencke et al. 2006). Tolerance of spores to UVR is a major if not one of the most important factors determining the upper depth distribution limit of kelps and kelp-like species. Enhanced UVR due to stratospheric ozone depletion may lead to changes in the depth distribution of seaweeds which may cause significant snowballing effects.

As temperature is one of the most important factors controlling biogeographic distribution of seaweeds, distributional shifts are an inevitable effect of global warming, especially in polar and cold-temperate regions (see Chap. 18 by Bartsch et al.). Modeled temperature changes through the end of twenty-first century indicate that North Atlantic-polar to cold-temperate seaweeds will extend their range into the high Arctic, but retreat along the northeastern Atlantic coasts. In contrast, many Antarctic seaweeds will presumably not strongly alter latitudinal distributions due to changes in temperature (Müller et al. 2011). Clearly, the distributional changes of key species as so-called ecological engineers will provoke substantial and cascading effects in polar and cold-temperate transition areas with strong consequences for biodiversity and ecosystem functioning.

Although increasing temperatures due to climate change may not affect the latitudinal distribution of Antarctic seaweeds directly, it very likely is doing so indirectly via changes in sea-ice extent and duration, particularly along the southern portion of the western Antarctic Peninsula. Sea-ice cover in this region has been dramatically changed by increases in air temperatures over the past 30 years, advancing nearly 2 months later in winter and retreating approximately 1 month earlier in spring (Smith and Stammerjohn 2001; Stammerjohn et al. 2008). These changes are likely to continue and are thought to be significantly impacting marine communities (Clarke et al. 2007; Ducklow et al. 2007; McClintock et al. 2008). The marked decrease in seaweed biomass and species richness historically observed along the southern portion of the Antarctic Peninsula is thought to be a result of the increasing sea-ice coverage as one moves south. It seems likely that seaweed communities typical of the northern portion of the western Antarctic Peninsula are expanding southward. Unfortunately, seaweed floras in the area between Anvers and Adelaide Islands (64°S–67°35′S) are very poorly studied, both historically and currently, so the extent to which such changes have and are occurring is unknown.

Polar regions are not only affected by stratospheric ozone depletion and global warming, but certainly also threatened by ocean acidification as a result of human use of fossil fuels (see Chap. 19 by Roleda and Hurd). When CO_2 enters the ocean surface, CO_2 and bicarbonate concentrations will increase, and in contrast, pH and carbon ion concentrations will decrease (Feely et al. 2004). As the solubility of gases is higher in colder waters, polar regions will be most strongly affected. In general, effects of ocean acidification on seaweeds and their communities are poorly understood. Elevated CO_2 levels may support primary production, although species with a carbon concentrating mechanism (Giordano et al. 2005) may show less strong responses. Calcification of calcareous algae will be impaired (Leclerc et al. 2000). For polar waters, there is only one publication addressing this important question (McClintock et al. 2009). Therefore, we need to study the responses of polar seaweeds to elevated CO_2 levels and ocean acidification in more detail and also investigate possible acclimation processes.

13.6 Conclusion

In the above summary of our present knowledge about polar seaweeds, gaps are clearly apparent. The biodiversity of polar algae must be studied more intensively to better understand their evolutionary history, biogeographical relationships, and their physiological performance. With respect to their phenology, an open question is the perception of daylength, which controls seasonal growth and reproduction in endemic Antarctic and Arctic seaweeds. Storage of photosynthetic products, their remobilization and translocation to the meristems, and prerequisites for growth in darkness and low light are not fully explored. Moreover, it is necessary to identify the thresholds of tolerance to low and high light, UV radiation, temperature, freezing, and other stresses and to quantify the related physiological processes by genomic, proteomic, and metabolomic approaches in order to better understand the ecology of individual species.

In seaweed communities from the Antarctic, the function of secondary metabolites in chemical defense and functioning of these systems need to be studied more intensively, not only with respect to herbivory, but also to biofouling. The putative photoprotective role of phlorotannins needs to be studied in greater detail. As the molecular structure of phlorotannins is still obscure, more studies are necessary also in this field. An improved knowledge of these compounds should allow us to investigate the effects of these brown algal secondary metabolites on grazers in a better way. In particular, the effects on the digestive system of consumers should come into the focus of science. Compared to Antarctic seaweeds, much less is known about seaweed–herbivore relationships in the Arctic, which therefore need to be studied much more intensively. Finally, the effect of global climate changes, especially of global warming and ocean acidification on seaweeds and their communities, must urgently be studied in order to develop scenarios about changes in the functioning of polar seaweed systems. In this respect, special emphasis should be laid on interactive effects between temperature, CO_2 level, pH, and radiation conditions to obtain a more plastic picture of future trends.

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Chapter 14
Cold-Temperate Seaweed Communities of the Southern Hemisphere

Pirjo Huovinen and Iván Gómez

Please note the Erratum to this chapter at the end of the book

14.1 The Regions and Their Basic Abiotic Conditions

In the southern hemisphere, two circumpolar fronts roughly define the boundaries of the cold-temperate region (Fig. 14.1). The southern limit, the Antarctic Polar Front (APF; also known as Antarctic Convergence), is characterized by cold (ranging 3–5°C) surface waters. The northern limit, the Subtropical Front (STF; also known as Subtropical Convergence), separates subtropical water in the north from sub-Antarctic water, and follows approximately the 10°C surface isotherm in winter and the 15°C surface isotherm in summer (Heath 1985; Parsons 1985; Lüning 1990; see also Chap. 3 by Eggert and Chap. 18 by Bartsch). The STF is a complex, irregular frontal zone with seasonal migration of up to 2° latitude (Nelson and Broom 2010). The large eastward-moving Antarctic Circumpolar Current (ACC; called also West Wind Drift) strongly determines the oceanography in the Southern Hemisphere (Orsi et al. 1995) (Fig. 14.1). The circulation of the ACC and circumpolar frontal zones strongly define the diversity, biogeography, and the ecology of seaweeds in all the adjacent coastal regions.

14.1.1 Southwestern South America Region

In the Southeastern Pacific coast of Chile, there are two major current systems, the southward Cape Horn Current and the northward Humboldt Current, derived from the ACC around 40°S (Fig. 14.1). In the south, the Cape Horn Current flows through the Drake Passage. Three major regions along the coast can be identified: the

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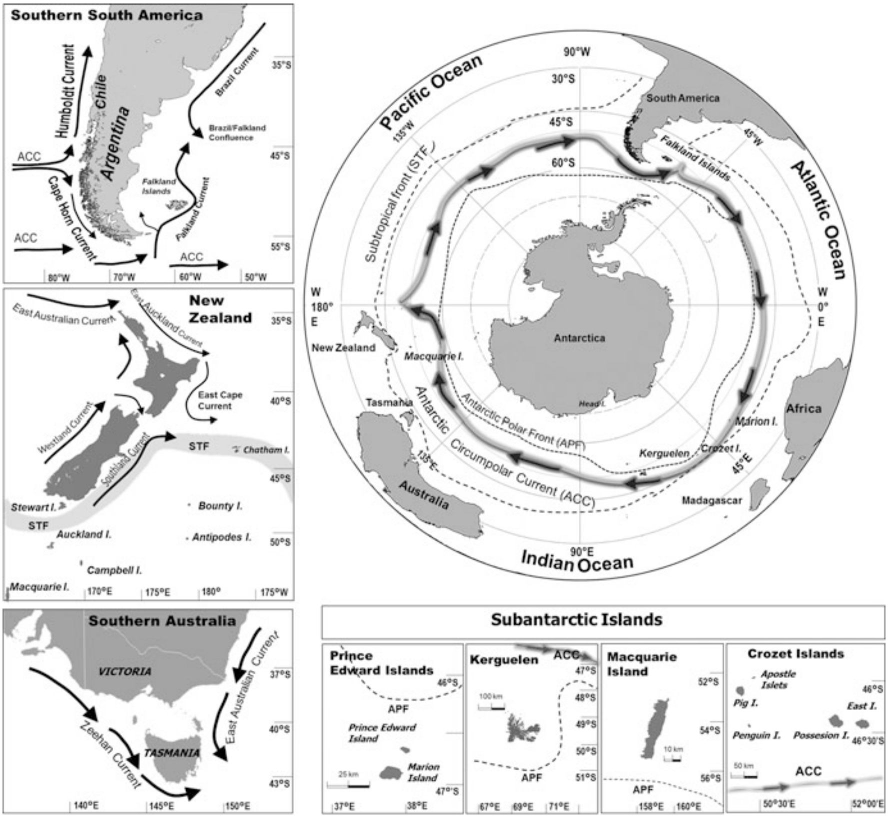

Fig. 14.1 The five cold-temperate regions of the southern hemisphere: southwestern South America, southeastern South America, Victoria-Tasmania, southern New Zealand, and the sub-Antarctic islands. Major oceanographic fronts, the Subtropical Front (STF; also known as Subtropical Convergence), the Antarctic Polar Front (APF; also known as Antarctic Convergence), and the Antarctic Circumpolar Current (ACC; called also West Wind Drift), are presented

southern Austral Fjords Region (sub-Antarctic, surface temperature 5–12°C), the Central/South Upwelling Region (Mediterranean characteristics, surface temperature 8–15°C), and the Northern Upwelling Region (subtropical, temperature 15–21°C) (Strub et al. 1998; Thiel et al. 2007; see also Chap. 18 by Bartsch). Habitats for seaweeds are characterized by exposed rocky shores between 18 and 41°S, while southwards the littoral systems exhibit higher variability with many fjords, archipelagos, and estuaries as well as glaciers (Santelices 1989).

14.1.2 Southeastern South America Region

In the coast of Argentina, the northward, cold-water (sub-Antarctic) Falkland current, derived from the ACC, meets the southward Brazil (subtropical) current around 36°S in an area called the Brazil/Falkland Confluence (Acha et al. 2004; Fig. 14.1). The cold-temperate section of the southeastern South America (approximately 41–55°S) is characterized by large bays and harbors, which provide heterogeneous habitats for seaweeds. Northwards of the Gulf San Matías (41°S), temperature increase and substrate become less suitable for seaweeds due to the massive runoff and sedimentation from Rio de la Plata (Acha et al. 2004). The Falkland Islands (Islas Malvinas), with sub-Antarctic characteristics, are situated in the path of the Falkland Current (Fig. 14.1) with water temperatures around 3–14°C (see also Chap. 18 by Bartsch). The coastal oceanography is characterized by the two branches of the Falkland Current, the weaker western branch (the Patagonian Current) rejoining the eastern branch north of the islands (Upton and Shaw 2002).

14.1.3 Victoria-Tasmania Region

The warm East Australian Current is the largest and the warm Leeuwin Current the second largest ocean current in Australia. The Leeuwin Current flows from the west Australian coast towards south-east, becoming the South Australia Current as it flows across the Great Australian Bight, reaching the west Tasmanian coast as the Zeehan Current (Fig. 14.1). The importance of these currents is evident from the tropical elements present in southern Australian waters at temperate latitudes. The southern coast of Tasmania is situated a few degrees north of the STF, the limit of sub-Antarctic waters (summarized by Poloczanska et al. 2007). However, in the coasts of Tasmania and Victoria, the surface water temperature remains cool, generally not exceeding 15°C in summer (Lüning 1990; see also Chap. 18 by Bartsch). The southern Australian coastline has large sections of rocky substrata, providing suitable habitats for seaweeds (Phillips 2001).

14.1.4 Southern New Zealand Region

Subtropical waters with relatively high salinity and temperature around New Zealand are mainly derived from the East Australian Current, while sub-Antarctic waters, with relatively low salinity and temperature, are driven north by the ACC. These two water masses meet in the STF (following roughly the 10°C winter and the 15°C summer surface isotherm; see also Chap. 18 by Bartsch). Along the east coast of the South Island, the Southland Current brings cool water towards north. It turns towards east and back to south around 40°S (Cape Turnagain), the northern limit for many species, combining with the warmer East Cape Current (Heath 1985; Parsons 1985) (Fig. 14.1). In the Fiordland region of the South Island, the exposed coastline is interrupted by channels, inlets, fjords, and many estuaries. Thus, the littoral systems in these locations are strongly influenced by the inflow of freshwater from rivers and glaciers (Nelson et al. 2002).

14.1.5 Sub-Antarctic Islands Region

The sub-Antarctic islands region consists of the island groups of Prince Edward (Prince Edward and Marion Islands), Crozet, Kerguélen, Heard (included also in the Antarctic region), and Macquarie (sometimes regarded in the Southern New Zealand region) Islands. The sub-Antarctic islands near New Zealand include Snares, Auckland, Campbell, Bounties, Antipodes, and Chatham Islands (Fig. 14.1). The location of the Southern Ocean islands in relation to the APF influences strongly their climatic conditions. Overall, these islands exhibit particularly cool, wet, and windy climates (Bergstrom and Chown 1999). The surface water temperatures along the coasts of the sub-Antarctic islands range 3–11°C in winter and 5–14°C in summer, depending on the geographical location (Lüning 1990).

14.2 Structure and Function of Seaweed Communities

14.2.1 Southwestern South America Region (Chile)

The southeastern Pacific coast can be divided into three biogeographic provinces: (1) the Peruvian province (from Peru to 30°S) with high presence of warm-temperate biota, (2) the Magellan province (from 40–42°S to 56°S) with dominance of sub-Antarctic cold-temperate elements, and (3) the intermediate area (from 30°S to 40–42°S) with mixed components from both provinces. According to Briggs (1974, cited in Lüning 1990) the cold-temperate region in the south-eastern Pacific is limited to the north at around 40°S (see also Chap. 18 by Bartsch et al.). Recent evidence (Strub et al. 1998; Camus 2001; Thiel et al. 2007) suggests that this region extends to around 30°S due to the influence of the Humboldt Current. In general, the seaweed flora in this region presents a remarkable degree of endemism (32%) (Santelices 1980), although recent accounts indicate increases in subtropical and alien species (Meneses and Santelices 2000; Castilla et al. 2005). Due to the higher occurrence of cold-temperate species, the total number of species increases southwards (Santelices 1980; Santelices and Marquet 1998). According to a recent update, the Magellan and Tierra del Fuego regions in the southern part of South America comprise 234 seaweed species (red 60%, brown 22%, green 18%) (Ramírez 2010). The species composition shows a break point around the latitude 42°S (Meneses and Santelices 2000).

In the wave-exposed coast at 30–55°S latitudes, the zonation and the structure of seaweed communities are characterized by the presence of *Porphyra columbina* and filamentous and foliose green algae such as *Ulva intestinalis* at upper littoral zones (Santelices 1989; Gómez and Huovinen 2011) (Fig. 14.2). In the mid-littoral, coarsely branched red algae such as *Mazzaella laminarioides and Nothogenia fastigiata* dominate. The red alga *Gelidium* sp. and the brown alga *Petalonia fascia*

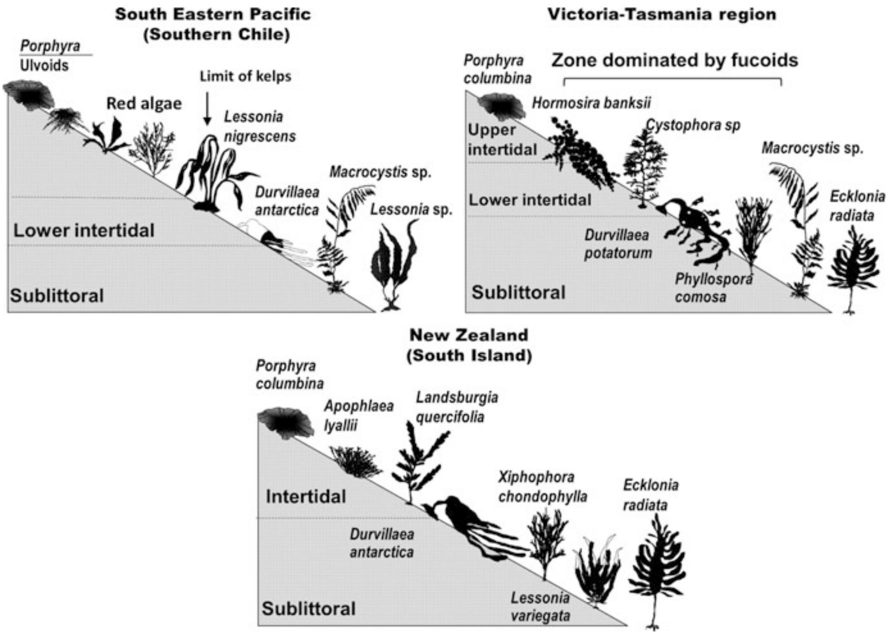

Fig. 14.2 General patterns of seaweed zonation, with dominant species in each littoral zone, in southern Chile, Victoria-Tasmania, and New Zealand (South Island) (the schemes represent a compilation of the literature revised in the text)

can colonize shaded pools and rocky crevices. The large kelp *Lessonia nigrescens* and the fucoid *Durvillaea antarctica* define the structure in the wave-battered infralittoral zone together with crustose/articulate species (*Corallina*) and red algae adapted to episodic erosion–accretion of sand such as *Ahnfeltiopsis durvillaei*. The sublittoral zone (up to 10 m) is characterized by a heterogeneous group with a dominance of kelps such as *Macrocystis pyrifera*, *Lessonia trabeculata*, *L. vadosa,* and *L. flavicans* (Villouta and Santelices 1986), mixed with thin leathery red algae (e.g., *Rhodymenia* sp. and *Callophyllis* sp.). Giant kelp forests are also found in protected bays and fjords, while the rhodophyte *Gracilaria chilensis* dominates in estuarine zones (Santelices 1980; Buschmann et al. 2004). At midlittoral and subtidal zones of the Magellan coast and some sub-Antarctic islands south of Tierra del Fuego (e.g., Diego Ramirez Islands), some species common to the Antarctic region (e.g., *Adenocystis utricularis*, *Iridaea cordata*, *Gigartina skottsbergii*, *Desmarestia* sp.) can be abundant (Santelices and Ojeda 1984; Westermeier and Rivera 1986).

The coexistence of *L. nigrescens* and *D. antarctica* at infralittoral zones conforms one of the most remarkable ecological associations. The spatial distribution and abundance of these two habitat-forming species result from complex interactions and morphofunctional adaptations, both species exhibiting different strategies to persist in areas with strong surf (Santelices et al. 1980; Westermeier et al. 1994). In general, factors determining the ecological functions of seaweeds have been well described for the ecosystems at 30–40°S (reviewed by Santelices 1989). At intertidal sites, trophic interactions with gastropods, such as the limpet *Fissurella*, the polyplacophoran *Chiton granossus,* and the snail *Tegula atra*, have important consequences for the seaweed communities (Moreno and Jaramillo 1983; Jara and Moreno 1984; Otaíza and Santelices 1985). At subtidal sites, the interaction between *M. pyrifera* and the sea urchins *Loxechinus albus* and *Tetrapygus niger* defines the ecological process of southern kelp forests (Santelices and Ojeda 1984; Dayton 1985). Unlike the situation for kelp forests of California, sea urchins from southern region preferentially consume algal drifts and act regulating the biomass of recruits (Moreno and Sutherland 1982; Vásquez et al. 1984; Graham et al. 2007). Some gastropods, such as *Tegula atra*, graze also on subtidal kelps (Moreno and Sutherland 1982; Buschmann 1992).

14.2.2 Southeastern South America Region (Argentinean Patagonia)

Approximately 400 seaweed species have been reported for the Atlantic coast of Argentina (reviewed by Lüning 1990). Two main biogeographical provinces have been proposed: (1) the Magellan province with cold water covering the southern Patagonia, and (2) the Argentinean province with warmer waters extending from North Patagonia (around Peninsula Valdés at 42–43°S) northwards (Lutz et al. 2003). In this region, species richness has been characterized as being relatively poor (Bolton 1994). Intertidal rocky shores here are characterized by a depauperate seaweed flora, mainly due to harsh physical conditions (Paruelo et al. 1998; Bertness et al. 2006), calcareous algae covering low tidal height in wave-protected sites (Bertness et al. 2006). Northwards from the Gulf San Matías (41°S), the massive runoff and sedimentation from Rio de la Plata limit the availability of hard substrates for seaweeds. In this region, temperate chlorophytes adapted to estuarine conditions dominate (Acha et al. 2004). Southwards, in the limit between the Argentinean and the Magellan biogeographical regions, subtropical species, such as *Dictyota*, are mixed with sub-Antarctic (e.g., *Bryopsis australis*) and endemic (e.g., *Myrogloia major*) components. The kelps *Macrocystis pyrifera*, *Lessonia flavicans,* and *L. vadosa* occur continuously from the Pacific to the Atlantic coast (up to 42°S for *Macrocystis*, 47–48°S for *Lessonia*) (Barrales and Lobban 1975; Searles 1978). The fucoid *Durvillaea antarctica* has its northern limit around 51°S in the Argentinean side of Tierra del Fuego (Boraso and Zaixso 2011). The invasive kelp *Undaria pinnatifida* has been associated with a decrease of species richness and diversity of native seaweeds in Patagonia (Casas et al. 2004; see also Chap. 12 by Andreakis and Schaffelke).

In the Falkland Islands, a total of 169 seaweed species (55% Rhodophyta, 29% Phaeophyceae, 16% Chlorophyta) were recently listed (Ramírez 2010). The lower intertidal zone is dominated by *Durvillaea antarctica*, while the subtidal zone is characterized by extensive *Macrocystis pyrifera* forests (van Tussenbroek 1993). Other large kelps, such as *Lessonia flavicans*, are also present (Ramírez 2010). Based on phylogenetic analyses, a highly diverse flora of bladed Bangiales (at least nine species) has been reported for the Falkland Islands (Broom et al. 2010). A high floristic similarity (60%) is found with the flora from Magellan-Tierra del Fuego region, principally due to species with a sub-Antarctic origin. The Falkland Islands and Magellan-Tierra del Fuego region form a group that separates from the Antarctic region (Hommersand et al. 2009; Ramírez 2010). These studies do not support the previously proposed biogeographic province with continuity of the marine flora in the Antarctic region and the sub-Antarctic South American region (John et al. 1994).

Ecological studies on seaweeds from the southeastern South American region are scarce, and thus the understanding of the distribution and abundance patterns as well as the functional roles of the seaweeds in these ecosystems is poorly known. Apparently, intertidal seaweed communities are strongly regulated by physical factors, as grazing pressure is weak due to the absence of common predaceous crabs and snails and the limited impact by limpets (Bertness et al. 2006). In subtidal environments, evidence based on population dynamics from Argentinean mainland and the Falkland Islands indicates that giant kelp beds are regulated by storms and nutrient availability (Barrales and Lobban 1975; van Tussenbroek 1989). In the kelp (*Macrocystis*) forests no consistent grazers, such as sea urchins, were reported either (Barrales and Lobban 1975). However, growth patterns and demography of these forests show considerable local variation (van Tussenbroek 1993).

14.2.3 Victoria-Tasmania Region

The seaweed flora of the southern Australia is characterized by high species richness and endemism (Bolton 1994; Phillips 2001; Kerswell 2006), resulting from a complex interaction of biogeographical, phylogenetic, and ecological processes (reviewed by Phillips 2001). Over 1,100 species (Bolton 1994) and four major floristic elements, i.e., endemic, widely distributed temperate, tropical, and polar elements, have been identified (Phillips 2001). Endemic (40–77%) and widely distributed temperate (17–45%) species account for the majority of the seaweeds, whereas species with tropical (4.5–9.7%) and polar (1.5–5.1%) affinities are much less represented. In Rhodophyta and Phaeophyceae, endemic elements dominate (77% and 59%, respectively), while in Chlorophyta widely distributed temperate (45%) flora account for the majority (Phillips 2001). Recent quantitative seaweed analyses confirmed the traditionally recognized Peronian (eastern), Flindersian (western), and Maugean (south-eastern) marine biogeographic provinces of the southern coast of Australia (Waters 2010). Furthermore, differentiation of marine communities in eastern and western elements has been associated with the Bassian Isthmus as a historical vicariant barrier (Waters 2008b; Fraser et al. 2009a).

The cold-temperate region of southern Australia (Victoria) and Tasmania is characterized by the dominance of fucoids, such as *Durvillaea potatorum* in the upper sublittoral zone in sites with high wave exposure (Cheshire and Hallam 1988) (Fig. 14.2). At medium-exposed sites the fucalean *Phyllosphora comosa* and the kelps *Macrocystis pyrifera* (former *M. angustifolia*) and *Ecklonia radiata* are common. In the intertidal zone, *Porphyra* dominate at higher locations, while at lower intertidal zones, the fucoid *Hormosira banksii* is abundant coexisting with green algae (e.g., *Codium*) and the Rhodophyta *Corallina*. Below the fringe of *H. banksii*, in the eulittoral zone *Cystophora torulosa* is the dominant fucoid. In southern Tasmania, *M. pyrifera* can form dense sublittoral forests in some locations, the upper sublittoral zone being dominated by *D. potatorum* and the endemic *Lessonia corrugata*. In general, many of the dominant fucoids are restricted to cold-temperate waters, and only *P. comosa* and *H. banksii* have distribution along the warm-temperate eastern coast of Australia (to a latitude 32°S). The northern limit of *D. potatorum* is at latitude 36°S, *M. pyrifera* (former *M. angustifolia*) extending to the northern border of Victoria (Lüning 1990).

Large brown algae, due to their size and foundational character, have been a special topic in many ecological studies (Sanderson and Thomas 1987). In the east coast of Tasmania, the sea urchins *Heliocidaris erythrogramma* and *Centrostephanus rodgersii* and the abalone *Haliotis rubra* regulate the population dynamics of various canopy-forming algae such as *Phyllospora comosa* and *Ecklonia radiata* (Valentine and Johnson 2005; Ling and Johnson 2009). Interestingly, the sea urchin barren zone is rapidly colonized by the introduced kelp *Undaria pinnatifida* (Valentine and Johnson 2004, 2005). In Tasmania, overgrazing of seaweeds by introduced sea urchin *Centrostephanus rodgersii* together with oceanographic changes is causing dramatic decline in the giant kelp beds (Johnson et al. 2011).

14.2.4 Southern New Zealand Region

Coasts of New Zealand represent areas of high seaweed diversity (Norton et al. 1996; Kerswell 2006). A recent account indicated that of the 770 currently known seaweed species, 265 are endemic (34%) and 22 alien (2.9%) (Hurd et al. 2004). According to the revision of Parsons (1985), the South Island hosts around 497 species, while for the North Island 555 species were reported. Rhodophyta accounts for around 60% of the total taxa, Chlorophyta and Phaeophyceae each contributing with approximately 20% (Parsons 1985). Within the cold-temperate southern New Zealand region are included the South Island, the southern part of the North Island, and the Stewart Island. Also the sub-Antarctic islands Auckland, Campbell, Antipodes, and Bounty, as well as the Chatham Island, are in this region (Fig. 14.2).

Although lower in number compared to green and red algae, brown algae, particularly fucoids, dominate the rocky shores of Southern New Zealand, while only few kelps can be regarded as dominant organisms (Schiel 1990) (Fig. 14.2). In the middle and lower intertidal zone, *Cystophora torulosa* and *Landsburgia* *quercifolia* are abundant, while *Durvillaea antarctica* is the most conspicuous brown alga in the lower littoral fringe at exposed sites, accompanied by red algae such as *Gigartina*, *Laurencia*, *Polysiphonia*, *Caulacanthus*, *Gelidium,* and *Nemalion*, the brown algae such as *Hormosira banksii* and *Colpomenia sinusosa*, and the green algae *Codium* and *Caulerpa*. In the southern part of the North Island (Wellington), the fucalean species *L. quercifolia*, *Carpophyllum flexuosum*, *C. maschalocarpum,* and *C. angustifolium* and the laminarian *Lessonia variegata* are common in shallow waters. *Macrocystis pyrifera* and *Ecklonia radiata* generally reach their highest abundance in deeper waters (Schiel 1990).

In Fiordland in the South Island, the lower intertidal is dominated by *Durvillaea antarctica,* particularly in the east coast. At around a depth of 2 m, the fucalean species *Xiphophora chondrophylla* is abundant. *Ecklonia radiata* is common at 3–6 m and at 12–18 m depth zones (Schiel 1990; Villouta et al. 2001). The upper sublittoral zone is inhabited by *Lessonia variegata* as well as *D. willana*, which is endemic to New Zealand (Cheshire et al. 1995). In sheltered rocky shores within the fjords, diversity and structure of seaweed assemblages have been less studied. Surveys carried out in Doubtful Sound (45°S) indicated the presence of, e.g., red alga *Pachymenia lusoria* and diverse *Ulva* species in the most estuarine locations. The lower intertidal zones are characterized by *D. antarctica*, *Xiphophora chondrophylla,* and sparse populations of *M. pyrifera* (Boyle et al. 2001).

The structure and function of seaweed communities from the New Zealand cold-temperate region, especially of fucalean and kelps, have been well addressed in some locations. However, many aspects of population dynamics and underlying processes such as phenology, dispersal, and recruitment have not been intensively addressed (reviewed by Hurd et al. 2004; Schiel 1990, 2004). On the other hand, biotic control of seaweed assemblages is different between regions from the main islands, which reflect their intrinsic differences in seaweed structure and composition (Schiel and Hickford 2001). For example, the impact of the sea urchin *Evechinus chloroticus* on different large brown algae is higher in northern communities dominated by *Ecklonia*, compared to communities dominated by cold-temperate seaweeds, e.g., in Fiordland and Chatham Island, where the *Ecklonia* stands are replaced by fucoids and other kelps such as *Lessonia* spp. (Schiel 1990; Villouta et al. 2001). The presence of large brown algae has different impact on understory species, especially red algae (Lilley and Schiel 2006), and in systems where the control by herbivores is less intense, the interspecific competence between large canopy-forming seaweeds can become a relevant factor (Schiel and Hickford 2001).

14.2.5 Sub-Antarctic Islands Region

According to a catalog of Papenfuss (1964), the seaweed flora of the sub-Antarctic islands and the Antarctic region contains 550 species, approximately half being endemic to these two regions, while approximately 75% of these species are distributed in the sub-Antarctic islands (Clayton 1994). These regions share a considerable number of cold-temperate species, e.g., the brown alga *Adenocystis utricularis*, the red alga *Iridaea cordata* and *Gigartina skottsbergii*, however, some endemic Antarctic species such as *Himantothallus grandifolius* and *Ascoseira mirabilis* do not inhabit the sub-Antarctic islands (Lüning 1990; Clayton 1994). The distribution of the endemic Antarctic rhodophyte *Palmaria decipiens* just extends to Macquarie Island (Wiencke and Clayton 2002). On the other hand, the circumpolar kelps *Macrocystis pyrifera* and *Lessonia* spp. as well as the large intertidal fucoid *Durvillaea antarctica* are absent from the Antarctic (John et al. 1994; Clayton et al. 1997).

The general zonation pattern for the shores of Macquarie Island has been described to comprise an upper littoral *Porphyra* zone, a "bare" zone (dominated by siphonariid mollusc *Kerguelenella lateralis*), an upper red algal zone (*Rhodymenia* sp., *Chaetangium fastigiatum*, *Palmaria georgica*, *Acrosiphonia pacifica*, *Porphyra columbina*), a kelp zone (*Durvillaea antarctica*), and lower red algal zone below the infralittoral with understory species such as *Delesseria* spp., *Iridaea* sp., and *Desmarestia* sp. (Kenny and Haysom 1962; Smith and Simpson 2002). Similarly, in Marion Island, *D. antarctica* is the dominant species at the infralittoral fringe, while *Desmarestia rossii* and *Durvillaea* sp. occur in a zone of 3–6 m. Encrusting coralline algae are particularly abundant in shallow areas (Beckley and Branch 1992). At subtidal locations, beds of the endemic *Macrocystis laevis* are abundant (Perissinotto and McQuaid 1992; Beckley and Branch 1992). In general, infralittoral *D. antarctica*, shallow-water encrusting coralline algae, *Desmarestia* spp., and subtidal *Macrocystis* beds seem to overall characterize the benthic seaweed communities in many sub-Antarctic islands (Beckley and Branch 1992).

For the sub-Antarctic islands near New Zealand, 14–148 seaweed species have been reported, with the highest species richness being recorded for Chatham Islands and the lowest for the Bounty Island (Parsons 1985). Although notable differences in species composition and dominance patterns can exist among islands (Freeman et al. 2011), *Durvillaea antarctica* and *Macrocystis pyrifera* occur in all these island groups, *Lessonia flavicans* reported for Auckland, Campbell, the Antipodes, and Bounty. The fucalean *Xiphophora chondrophylla* is present in all the island groups, except for the Bounty (Lüning 1990). Endemic *Durvillaea* species have been proposed for the Antipodes (undescribed species) and Chatham Island (*D. chathamensis*) (Cheshire et al. 1995; Fraser et al. 2010b; Fig. 14.3). In the light of a re-examination of the description of *Porphyra columbina* using molecular techniques, this species is distributed in the Auckland, Campbell, Antipodes, Chatham, and Falkland Islands, with a very restricted distribution in mainland New Zealand (Nelson and Broom 2010).

In the Chatham Island, the shallowest subtidal areas are dominated by *Durvillaea*. Several fucalean species (e.g., *Xiphophora chondrophylla*, *Carpophyllum plumosum* and *C. maschalocarpum*) are abundant to a depth of around 10 m, *C. flexuosum* occurring mostly in deeper waters (9–20 m). The endemic *Lessonia tholiformis* and *L. variegata* are abundant at 2.5–15 m depth. In some sites, *Macrocystis pyrifera* forms dense beds at 15–20 m depth. In the Auckland Islands,

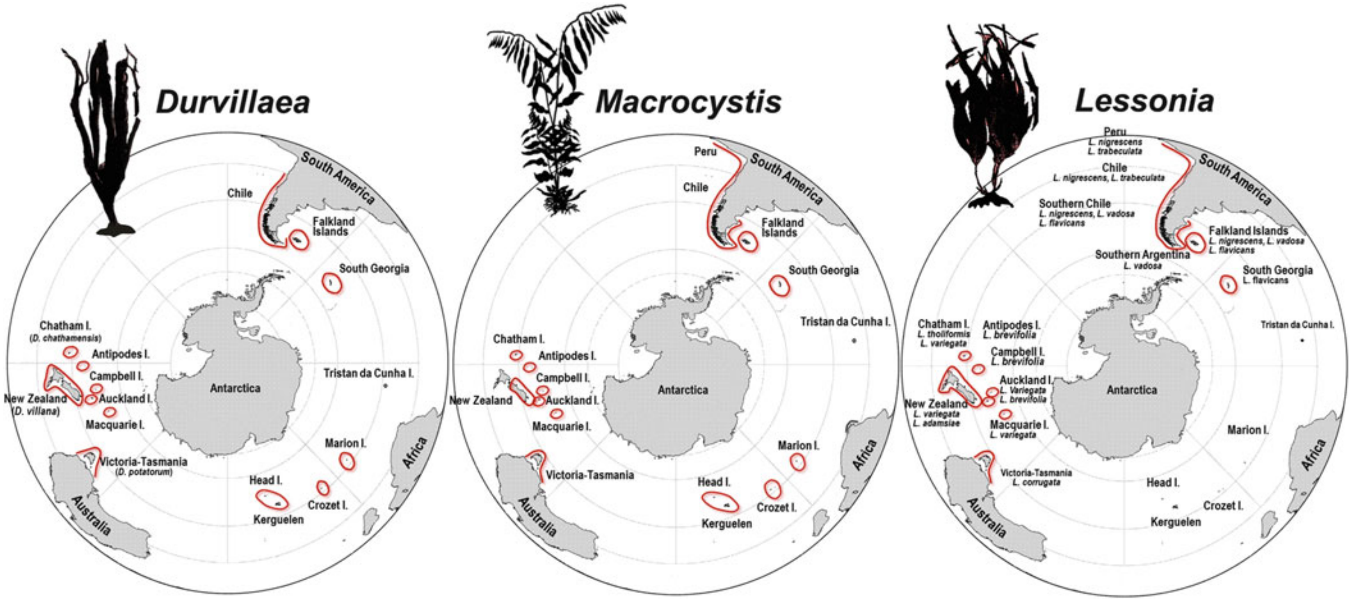

Fig. 14.3 Distribution of the large brown algal genera *Durvillaea* and laminariales *Macrocystis* and *Lessonia* in the southern hemisphere. Different species of *Durvillaea* and *Lessonia* are presented. As the current evidence indicates the existence of only one species of *Macrocystis* (*M. pyrifera*) (see the text), this information is presented as *Macrocystis* sp. Note: *Macrocystis* is also present in the northern hemisphere in the Pacific coast from Baja California, Mexico, to Alaska (the schemes represent a compilation of the literature revised in the text)

shallowest areas are also dominated by *D. antarctica*. *Xiphophora* is common at 2 m depth and *Halopteris funicularis* around 2–5 m. *Lessonia brevifolia* forms beds around 4–12 m depth, *M. pyrifera* being abundant in deep waters. The laminarian *Ecklonia radiata,* the most common kelp of New Zealand, has not been recorded neither at the Chatham nor the Auckland Islands (Schiel 1990; Schiel et al. 1995).

The ecology of the seaweed communities from the sub-Antarctic islands region is poorly known. The harsh environmental conditions as well as the remoteness and inaccessibility of many islands impede experimental studies. The scarce studies characterizing the structure and functions of seaweeds of intertidal zones reveal that physical environmental factors exert a strong control on these assemblages, probably regulating also the action by herbivores (Smith and Simpson 2002; Freeman et al. 2011). On the other hand, the importance of the habitat-forming species *Durvillaea antarctica* on the ecology of the littoral system has been emphasized (Klemm and Hallam 1988; Smith and Simpson 2002). In subtidal areas of these islands, the biological processes occurring within the *Macrocystis* forests have been also studied (Dayton 1985; Graham et al. 2007), including aspects related with their trophic role in the food web (Kaehler et al. 2006), aspects of primary production, and geochemical cycles (Delille et al. 2009).

14.3 Biogeographical Processes

The development of the ACC as a result of the opening of the Tasmanian Gateway between Australia and Antarctica (~33 Ma) and the Drake Passage between South America and Antarctica (~23 Ma) permitted the circumpolar distribution of biota in the southern hemisphere (Clayton 1994). Many cool water taxa evolved in the early Tertiary at high latitudes (the so-called Weddellian species) and colonized lower latitudes, e.g., Tierra del Fuego in southern South America (Lüning 1990). A relatively recent long-range dispersal across the Southern Ocean is reflected in many species reported in South America, the Falkland Islands, and various sub-Antarctic islands (Clayton 1994; see also Chap. 17 by Rothäusler et al.).

In order to interpret the present distribution patterns and origin of biota in the southern hemisphere, different theories dealing with separation through plate tectonics, long-distance dispersal during different periods, and the role of the formation of the ACC linking the land masses have been proposed over the last decades. Models of the species distribution involving ACC dispersal were widely replaced by vicariance and the role of past geological events (plate tectonic) (Cheshire et al. 1995; Waters 2008a). However, recent evidence based on new molecular techniques emphasizes the role of dispersal in distribution of marine biota in the southern hemisphere and relates some evidence of vicariance in southern waters with more localized and recent vicariant models, e.g., the isolation by the Bassian Isthmus that connected Tasmania with Australia during Pleistocene low sea-level, rather than with plate tectonics (Waters 2008a; Fraser et al. 2009a). Recent ecological, phylogenetic, and phylogeographic studies suggest also that rafting cannot be ignored as an important mechanism of long-distance dispersal in southern waters (Waters 2008a; see also Chap. 17 by Rothäusler et al.).

14.3.1 Cold-Temperate Kelps as Biogeographical Models

The large “bull kelp” *Durvillaea* has proved to be an interesting model for seaweed biogeography. This genus has five recognized species: one (*D. antarctica*) is buoyant and with circumpolar distribution, while other four are nonbuoyant and with restricted distribution (*D. willana* present in southern New Zealand, *D. potatorum* in southern Australia and Tasmania, *D. chathamensis* in Chatham Islands, an undescribed species *Durvillaea* sp. in Antipodes Islands) (Cheshire et al. 1995) (Fig. 14.3). Recently, a phylogeographic circum-sub-Antarctic study provided evidence of recent (postglacial) recolonization by *D. antarctica*, most probably by transoceanic rafting of adult specimens (see also Chap. 17 by Rothäusler et al.). This is supported by high genetic homogeneity over vast geographic distances in sub-Antarctic latitudes, while along the coasts of New Zealand and Chile, substantial genetic differentiation was detected over relatively small geographic distances (e.g., tens of kilometers) (Fraser et al. 2009b).

In the coast of Chile, two different lineages of *D. antarctica* with a biogeographic break at 44–49°S have recently been revealed. Interestingly, populations from southern Patagonia (49–56°S) were found to be genetically homogenous and identical to a haplotype found throughout the sub-Antarctic region, pointing to the transoceanic ancestry and a relative recent recolonization (since the Last Glacial Maximum) (Fraser et al. 2010a). Similarly, genetically distinct species have been postulated for two populations of *D. antarctica* in New Zealand (Fraser et al. 2009c). Under a phylogenetic species concept, the genus *Durvillaea* has been recently interpreted as a complex of nine distinct evolutionary lineages, only one of which has an intercontinental distribution (Fraser et al. 2010b).

The most widely distributed kelp, *Macrocystis* (Fig. 14.3), displays an amphi-equatorial distribution. Four species (*M. pyrifera*, *M., integrifolia*, *M. angustifolia,* and *M. laevis*) are currently recognized, however, increasing evidence strongly suggests the existence of a single morphologically plastic species (reviewed by Graham et al. 2007; Demes et al. 2009). Phylogenetic analyses by Coyer et al. (2001) point to a very recent (0.01–3 Ma) dispersal of *Macrocystis* from the northern to the southern hemisphere. This direction of the dispersal was supported by the greater genetic diversity of the individuals of the northern hemisphere, displaying paraphyletic clades, while the southern individuals formed monophyletic clades and showed little genetic differentiation across a wide southern geographic range, which refers to a recent dispersal.

Unlike the floating *D. antarctica*, the species of the genus *Lessonia* show a disperse distribution along the southern hemisphere (Fig. 14.3) characterized by a remarkable regional endemism (Searles 1978). The only intertidal species, *L. nigrescens*, extends from 17°S to 56°S and is the dominant organism at the infralittoral zone of the wave exposed locations of Chile and Peru (Santelices 1989). The subtidal *L. trabeculata* has a distribution range from 12 to 41°S in the eastern Pacific coast (from Peru to Chiloé Island) (Villouta and Santelices 1986). Populations of *L. vadosa* are found in the southern South America (47–56°S) in the coasts of Chile and Argentina as well as in the Falkland Islands (Searles 1978; Scrosati 1991). *L. flavicans* has also been described for South Georgia (John et al. 1994). *L. variegata* is endemic to New Zealand region including the mainland (Schwarz et al. 2006) and some adjacent islands (Chatham, Auckland, and Macquarie) (Kenny and Haysom 1962; Hay 1981). Other species show restricted distribution in this region, *L. tholiformis* being *e*ndemic to Chatham Island (Hay 1989), *L. brevifolia* present in Auckland, Campbell, Antipodes, and Bounty Islands (Hay 1981, 1987), *L. adamsiae* in Snares Islands (Hay 1987), and *L. corrugata* in Tasmania (Lane et al. 2006) (Fig. 14.3).

Recent phylogeographic analyses indicated the presence of two main divergent lineages, possibly two cryptic species, within *L. nigrescens* of the coast of Chile (Tellier et al. 2009), which matches the biogeographical transition zone around 30°S. In this species complex, a very limited dispersal has been reported (Faugeron et al. 2005; Tellier et al. 2009), confirming the marked endemism in many regions. Apparently, environmental factors (e.g., temperature) and anthropogenic activities can reduce gene flow between populations of *L. nigrescens* (Faugeron et al. 2005; Oppliger et al. 2011). Despite some molecular analyses (Lane et al. 2006), the origin of the genus *Lessonia* still remains unclear. Interestingly, within Lessoniaceae, it is the only genus not present in the northern hemisphere, and furthermore, it does not appear to be closely related to the other genera of this family (Bolton 2010).

14.4 Major Differences with Cold Temperate Regions of the Northern Hemisphere

Cold-adapted seaweeds are believed to have developed during the Tertiary decline of seawater temperature in temperate and polar regions. A permanent separation of the southern and northern hemisphere cold-water flora was produced by the formation of the pan-tropical Tethys Sea during the Mezozoic era (251–65 Ma). The presence of amphi-equatorial species with cold-temperate characteristics might be the result of processes such as paleoclimatic vicariance during the Miocene when intrusion of glacial water masses allowed many species crossing the equator (Lüning 1990; see also Chap. 18 by Bartsch et al.). However, some evidence indicates that disjunctions for some species are of a recent origin, e.g., during the last Pleistocene glacial maximum (18,000 years ago) (van Oppen et al. 1994). In the genus *Macrocystis*, phylogenetic analyses point to a very recent (0.01–3 Ma) dispersal from the northern to the southern hemisphere (Coyer et al. 2001). These transequatorial migrations took place at the east side of the oceans where the tropical regions are compressed. Crossing the equator was facilitated by "stepping stones," as well as by further constriction of the tropical regions during the Pleistocene and by glacial temperature drops as high as 8°C (reviewed by Lüning 1990; see also Chap. 18 by Bartsch et al.).

Compared to the cold-temperate regions in the northern hemisphere, the southern hemisphere has been characterized by the greater importance of the prevailing ocean currents for the seaweed distribution as well as by a more pronounced geographical isolation of the seaweed flora (Lüning 1990). In the southern hemisphere, the cold temperate regions have more island-like or peninsular character, thus resulting in a higher endemism. In the northern hemisphere, migrations at higher latitudes are possible mainly along coastlines. Since its formation the ACC has been the dominating biogeographical element at cold-temperate latitudes of the southern hemisphere and has served as a migration route for floating seaweed species (e.g., *Macrocystis pyrifera* and *Durvillaea antarctica*) creating similarities in floras between these regions (Lüning 1990; Fraser et al. 2009a; see also Chap. 17 by Rothäusler et al.).

One of the striking differences between the northern and southern cold-temperate regions is the almost exclusive dominance of species of the order Laminariales in littoral systems in the northern hemisphere, whereas in the southern hemisphere the only genera of the Laminariales, i.e., *Macrocystis*, *Lessonia*, *Ecklonia*, *Eisenia,* and *Laminaria*, grow intermixed with various dominant fucalean species. Nearshore reef assemblages in temperate New Zealand and Australia differ from those in other parts of the world: fucalean seaweeds dominate in the shallow subtidal zone, the kelp *E. radiata* forms dense beds at middle depths, and the giant kelp *M. pyrifera* occurs in the southern regions, but is abundant at only a few sites (Schiel et al. 1995). In the mid-intertidal zone, *Chondrus crispus*, a common dominant rhodophyte in the northern hemisphere, is replaced in regions of southern South America and many sub-Antarctic islands by species of *Nothogenia* and by the brown alga *Adenocystis utricularis* (Westermeier and Rivera 1986; Ingólfsson 2005). Among the main similarities between the northern and southern hemisphere cold-temperate floras is the presence of various members of the order Desmarestiales. In the coast of southern Chile, South Africa, and many sub-Antarctic islands several species of *Desmarestia* are regional endemics, and some species such as *D. ligulata* and *D. confervoides*/*D. viridis* exhibit a disjunct amphi-equatorial distribution (Wiencke et al. 1994; Peters et al. 1997). Species such as *D. anceps*, *D. menziesii,* and *Himantothallus grandifolius* are dominant in the Antarctic, but absent from the cold-temperate region. These species are regarded as ecological equivalent of Laminariales in the northern hemisphere (Moe and Silva 1977; Clayton 1994; Wiencke et al. 1996).

14.5 Concluding Remarks

Seaweed flora in the cold-temperate regions of the southern hemisphere has been modified not only by large-scale geological and paleoclimatic processes but also by long-distance dispersal events and an inherent capacity of the species to adapt to new habitats. Diverse present and future threats arising from anthropogenic activities will impose new challenges for these seaweeds communities. Many related aspects, such as temperature rise (see also Chap. 18 by Bartsch et al.), ocean acidification (see also Chap. 19 by Roleda and Hurd.), stratospheric ozone depletion and solar UV-B radiation (see also Chap. 20 by Bischof and Steinhoff), marine eutrophication and pollution (see also Chap. 21 by Teichberg.), as well as invasive seaweed species (see also Chap. 12 by Andreakis and Schaffelke.) and aquaculture (see also Chap. 22 by Buchholz et al.), are addressed in more detail in separate chapters throughout this book.

One of the most important issues is the scarce basic knowledge on the seaweeds communities over large areas. Although advances have been made in some regions, such as central/southern Chile, southern Australia, and New Zealand, seaweed communities of, e.g., the fjord region of southern Chile, the Argentinean region, and many sub-Antarctic islands are poorly known, partly due to their remoteness. The lack of studies on species diversity, community structure, and function of seaweeds in these locations impede suitable estimations on their contribution to the global geochemical fluxes, the potential genetic loss due to environmental shifts, and, in general, their conservation status. These are basic elements to understand the potential for tolerance and resilience in scenarios of global change (Harley et al. 2006).

Due to the closeness of the Antarctic ozone hole, the increase of solar UV-B radiation and resulting adverse effects on the biota of the cold-temperate region in the southern hemisphere is of a concern. Considering the latitudinal gradients of UV radiation and episodes of stratospheric ozone depletion reaching latitudes as low as 40°S (Orce and Helblin 1997), it is reasonable to argue that this factor can impose geographical barriers to species exhibiting low stress tolerance capacity. Recently, the potential effects of enhanced ultraviolet radiation on seaweed physiology have been examined in the context of adaptations to the intertidal life both in the Pacific and Atlantic coasts of Patagonia (Häder et al. 2003; Gómez et al. 2004; Huovinen et al. 2006; Rautenberger et al. 2009; Huovinen and Gómez 2011).

In some islands of the Southern Ocean, especially in Marion, Kerguelen, and Macquarie Island, a marked climate change, expressed as increases in temperature and declines of precipitation, has begun to be examined in the context of global warming. Because of the closeness of these islands to the APF, a relatively mobile climatic boundary, the impact of these climate shifts and its relation with, e.g., invasion of species in these islands has drawn attention, hitherto for terrestrial ecosystems (Bergstrom and Chown 1999). In Tasmania, intensification of southward intrusions of warmer, nutrient-poor East Australian Current waters has been reported to cause ocean warming and transport of biota to eastern Tasmania. The shift in large-scale oceanography has been related with a decline in the extent of the giant kelp beds. Furthermore, overgrazing of seaweeds by a recently established sea urchin species is affecting fundamentally the rocky reef systems in Tasmania (Johnson et al. 2011).

As seaweed communities of the cold-temperate region in the southern hemisphere are relatively isolated and thus, their structure, function, and biogeographic processes are strongly dependent on the environmental context, the direct impact of human activities requires urgent attention. Important questions related with impact of fish aquaculture and industrial effluents, introduction of alien species, and the overexploitation of commercially important seaweeds have not been addressed in detail. This information clearly is essential in order to understand the ecological processes of these organisms and their adaptive potential to large-scale physical forcings.

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Chapter 15
Warm Temperate Seaweed Communities: A Case Study of Deep Water Kelp Forests from the Alboran Sea (SW Mediterranean Sea) and the Strait of Gibraltar

Antonio Flores-Moya

15.1 Introduction: Kelp Forests and Kelp Beds in the Alboran Sea and the Strait of Gibraltar

Kelp forests dominate the shallower sublittoral of temperate oceans worldwide (Mann 1973; Dayton 1985, 1994; Steneck et al. 2002) although they are also present in the Arctic Ocean (Dunton et al. 1982; Steneck et al. 2002; see also Chap. 13 by Wiencke and Amsler) and in deep waters near Ecuador (Graham et al. 2007). There are singular kelp forest communities inhabiting deep waters (20–100 m depth) in some localities at the Strait of Gibraltar and in the Mediterranean Sea, e.g., the Alboran Sea (the westernmost portion of the Mediterranean Sea; Flores-Moya 2004; Templado et al. 2006) and the Strait of Messina (SW Italy; Huvé 1958; Fredj and Giermann 1969; Giaccone 1969, 1972; Drew 1972, 1974).

Curiously, the first record of the presence of kelps in the areas close to the Strait of Gibraltar may be due to the "Father of Botany," Theophrastus of Eresus (371–286 BC): "Again in the ocean, about the Pillars of Hercules, there is a [seaweed] kind of marvelous size, they say, which is larger, about a palmsbreadth. This is carried into the inner sea along with the current from the outer sea, and they call it "sea-leek"; and in this [outer] sea in some parts it grows higher than a man's waist" (translation of Hort 1926). The "Pillars of Hercules" are peaks at either side of the Strait of Gibraltar, while the Atlantic Ocean and the Alboran Sea can be recognized as the "outer sea" and "inner sea," respectively. Drift thalli of *Saccorhiza polyschides* are very frequent in the autumn and winter on the beaches of the area; thus, this species is possibly the best candidate for Theophrastus

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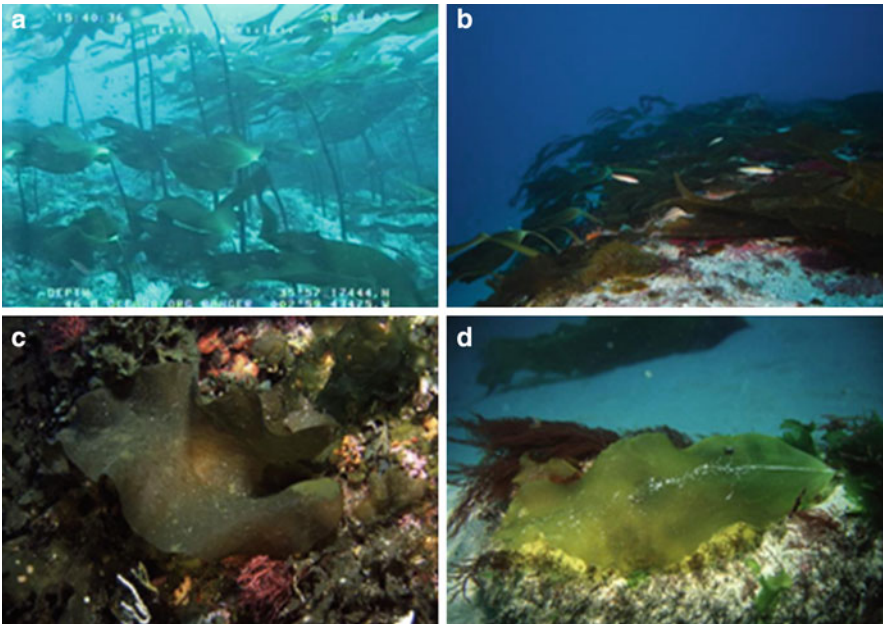

Fig. 15.1 Kelp forest of *Laminaria ochroleuca* (**a**) at 46 m depth at Alboran Island and *Saccorhiza polyschides* (**b**) at 24 m depth at Tarifa (Strait of Gibraltar). *Phyllariopsis brevipes* (**c**) at 42 m depth at Tarifa (Strait of Gibraltar). *Phyllariopsis purpurascens* (**d**) at 45 m depth at Tarifa (Strait of Gibraltar). Photographs courtesy from OCEANA (**a**) and from JC Moreno (**b**–**d**)

"sea-leek" (Amigues 1989). However, the first evidence of the presence of kelp forests in the Mediterranean Sea (in particular at Alboran Island, located at the center of the Alboran Sea) was found in 1958 in the course of dives by an expedition of the vessel *Calypso* (Cousteau and Dugan 1963). Before this discovery, it was thought that kelp forests were not present in the Mediterranean Sea. These forests remain poorly studied in comparison to similar communities in other oceans due to their locations in deep waters and the few phycologists working on this area.

The species occurring in the deep water kelp forests are *Laminaria ochroleuca* Bachelot de la Pylaie, *S. polyschides* (Lightfoot) Batters, and the small kelps *Phyllariopsis brevipes* (C. Agardh) E. C. Henry & G. R. South and *Phyllariopsis purpurascens* (C. Agardh) E. C. Henry & G. R. South, which also form open kelp bed communities in very deep waters. While *L. ochroleuca* is a member of Laminariales, the other three species are members of Phyllariaceae, a family that has been transferred from Laminariales to Tilopteridales (Sasaki et al. 2001; Adl et al. 2005).

L. ochroleuca (Fig. 15.1a) inhabits the NW Atlantic Ocean (from Brittany and South England in the North to the Atlantic shores of Morocco in the South); it is also present in the Azores, the Alboran Sea, and the Strait of Messina and, in the southern hemisphere, in Namibia (detailed references on distribution of all of the

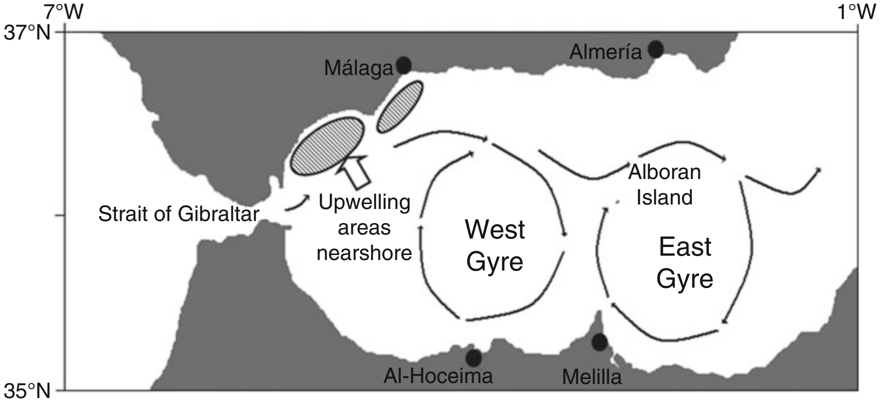

Fig. 15.2 Main surface currents and upwelling zones in the Strait of Gibraltar and the Alboran Sea

cited species are available in Guiry and Guiry 2011). The perennial thalli have a holdfast with branched haptera, a stipe (in the longest individuals reaching 3 m length) and a blade (up to 3–4 m length) divided into laciniae.

S. polyschides (Fig. 15.1b) is a North Atlantic species (from the Norwegian shores at the North to Mauritania at the South) that can also be found in the Canary Islands and in deep waters from the Alboran Sea and the Strait of Messina. It has a holdfast with a large bulb and small unbranched haptera, a stipe with lateral frills, and a blade divided into laciniae. Thalli are smaller than those of *L. ochroleuca*, but they can reach 3–4 m length. This species is annual or biennial.

Both species of *Phyllariopsis* are annuals and inhabit the NW and W Iberian Peninsula, NW Morocco, the western Mediterranean Sea, and the Strait of Messina, but *P. purpurascens* has also been found in the Canary Islands. *P. brevipes* (Fig. 15.1c) has an entire, cordate blade of <0.5 m length and a short stipe; the holdfasts have unbranched haptera. *P. purpurascens* (Fig. 15.1d) has a single blade that, in the longest individuals, reaches 2 m in length. It holds to the substratum by a disc of around 1 cm diameter, and it has a stipe 10–12 cm in length. The Mediterranean endemic *Laminaria rodriguezii* Bornet inhabits very deep waters (50–120 m depths) in the Western Mediterranean Sea and in the Adriatic Sea (Feldmann 1934; Giaccone 1969), but this species has not been found in the Alboran Sea (Pérez-Ruzafa et al. 2003).

The presence of kelp forests and beds in the Alboran Sea and the Strait of Gibraltar is linked to the particular oceanographic conditions (Fig. 15.2). The negative water balance in the Mediterranean Sea (i.e., the loss of water by evaporation is higher than the inputs by precipitation and rivers) is compensated by a permanent current flowing from the Atlantic Ocean into the Mediterranean Sea across the Strait of Gibraltar. Thus, the salinity in the Mediterranean Sea is higher than that at the same latitude in the neighbor Atlantic Ocean, but it does not increase further because high-salinity deep water current flows from the Mediterranean to

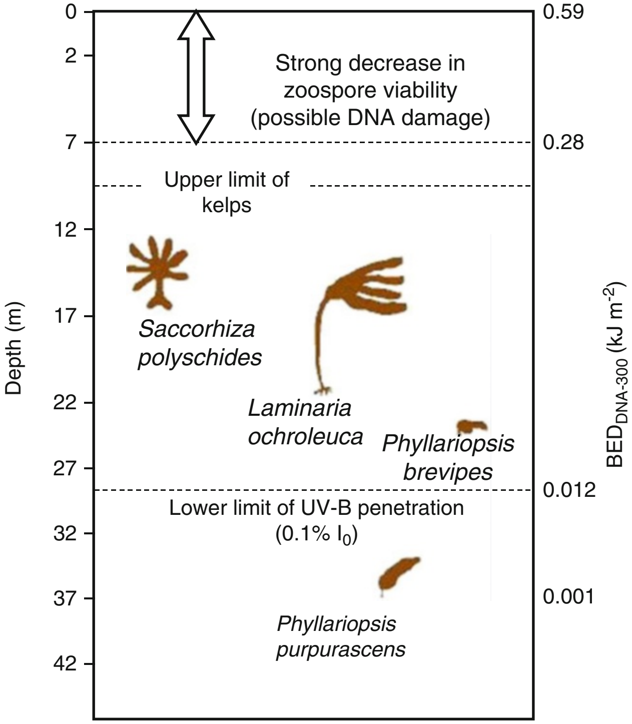

Fig. 15.3 Zonation of the four kelps at Tarifa (Strait of Gibraltar) and its correlation to the prevailing vertical ultraviolet-B radiation conditions and major biological and bio-optical events, expressed as biologically effective ultraviolet-B doses for DNA damage (BED$_{DNA-300}$) assuming constant photon fluence rates during 8 h (Wiencke et al. 2000)

the Atlantic. The surface current of Atlantic water flows close to the shores of the Iberian Peninsula and then it turns around, like an anticyclone, in the Western Alboran Sea. Simultaneously, upwelling of cold, deep water close to the shores compensates for the accumulation of water by the action of the anticyclone (Lacombe and Tchernia 1972; Rodríguez 1982; Sarhan et al. 2000).

The kelp forests are located in the Strait of Gibraltar, in the cold and nutrient-rich upwelling zones close to the South Iberian Peninsula, similar as in other kelp regions worldwide (Druehl 1981; Bolton 2010; Steneck et al. 2002) and at Alboran Island. Because of the high number of sunny days in the Mediterranean and the high light transmittance of the clear water, kelp forests are confined to deep water as a consequence of the photoinhibitory effects of the strong irradiance in shallow water (see Fig. 15.3). Moreover, surface temperatures >22°C in summer also contribute to the restriction in depth because these high temperatures are at the edge of thermal limits for the kelp species inhabiting Alboran Island (see Table 15.1).

Table 15.1 Growth and reproduction thermal limits for the kelps inhabiting the Strait of Gibraltar and the Alboran Sea

Species	Growth/reproduction (sporophyte)		Growth/reproduction (gametophyte)		References
	Upper	Lower	Upper	Lower	
Laminaria ochroleuca	22–23°C/*	*/*	*/21°C	*/5°C	Lüning (1990), Izquierdo et al. (2002)
Saccorhiza polyschides	24°C/*	3°C/*	25°C/<17°C	+/5°C	Norton (1970)
Phyllariopsis brevipes	*/*	*/*	20°C/20°C	10°C/10°C	Henry (1987)
Phyllariopsis purpurascens	*/*	*/*	20°C/20°C	10°C/10°C	Unpublished

Lethal limits can be estimated 1–2°C beyond the growth thermal limits
Asterisks: no data are available

15.2 Abiotic Factors Affecting Distribution of Kelps in the Alboran Sea and the Strait of Gibraltar

15.2.1 Substratum

The four species of kelps inhabit hard substrata. A singular case is *P. brevipes*, which always grows on living thalli of the crustose coralline *Mesophyllum alternans* (Foslie) Cabioch & Mendoza (Henry 1987; Pérez-Cirera et al. 1989). The specificity for the substratum in *P. brevipes* is possibly due to the requirements of the microscopic gametophyte (Sauvageau 1918) rather than to those of the sporophyte.

15.2.2 Hydrodynamics

The bottoms where kelps grow in the Strait of Gibraltar are exposed to very strong currents linked to the semidiurnal tidal cycle, with peaks of 2.5 m s^{-1} at low or high tide at spring tides (Lacombe and Richez 1982). The current may be a factor controlling the largest blade area that kelps can reach. Blades of 0.1 m^2 of *P. purpurascens* (the largest blade area found) can be detached from the stipe with current velocities ranging from 2.4 to 3.5 m s^{-1} and an inverse correlation was detected between blade area and current exposure on different bottoms (Flores-Moya et al. 1993; Flores-Moya 1997). A similar control by peak currents decapitating older thalli was suggested for *L. ochroleuca* in the Strait of Messina (Drew et al. 1982).

15.2.3 Irradiance

It is accepted that the lower limit of distribution of kelps corresponds to approximately 1% of the surface solar irradiance (Lüning and Dring 1979) and this assessment agrees with the maximum depths found for the kelps from the Alboran Sea and the Strait of Gibraltar. The lower limit of *L. ochroleuca* in the Strait of Gibraltar (Jerlov's optical water oceanic II–III and coastal 1–2 types) is close to 25 m depth, but at Alboran Island (Jerlov's optical water oceanic I–II type) it reaches 70–80 m depth (Flores-Moya 2004; Templado et al. 2006; Aguilar et al. 2010). There is a report of possible heterotrophic growth of *L. ochroleuca* in deep water from the Strait of Messina (Drew et al. 1982), but data are inconclusive. The most complete set of data about irradiance requirements was derived from a study of the sporophyte of *P. purpurascens*. The compensation of dark respiration by photosynthesis is achieved at 6.5 μmol photons m^{-2} s^{-1}. This irradiance level occurs at 35–40 m depth in summer, the lowest limit of the deepest populations in the Strait of Gibraltar (Flores-Moya et al. 1995). Similarly, the compensation irradiance occurs at 85–100 m depth at Alboran Island (Templado et al. 2006; Aguilar et al. 2010). This is the reason why this kelp and, in general, the four species cited in this chapter must be recognized as "shade plants" (see also Chap. 1 by Hanelt and Figueroa). Moreover, it can be hypothesized that the irradiance requirements of the gametophytes are lower than for the sporophytes, although no data are available.

Although the high PAR levels are usually considered to be responsible for determination of the upper depth limit of sublittoral seaweeds (Lüning and Dring 1979), the ultraviolet-B radiation (UV-B) also affects the germination of zoospores and the growth of microscopic gametophytes of kelps. Thus, the capacity to tolerate UV-B by zoospores and gametophytes of the four kelps in the Strait of Gibraltar is correlated with those levels of solar UV-B that penetrate seawater column (Fig. 15.3; Wiencke et al. 2000; Roleda et al. 2004; see also Chap. 20 by Bischof and Steinhoff). This could also be the reason for a deeper upper limit of kelps at Alboran Island, because the water there is more transparent than in the Strait of Gibraltar (see above).

15.2.4 Temperature

In the deep waters where kelps occur in the Alboran Sea and the Strait of Gibraltar (below 20 m depth), temperature never exceeds 15°C in summer. Thus, the thermal regime is closer to those of cold temperate oceans than to warm temperate ones. Moreover, this habitat is very constant in temperature. For instance, the temperature in the Strait of Gibraltar at 35–45 m depth (where *P. purpurascens* form kelp beds) ranges from 12.5 to 14.5°C during the year (Flores-Moya et al. 1993; Flores-Moya 1997).

The thermal limits for growth and reproduction of the four species are compiled in Table 15.1, but no data are available on the lethal limits. Moreover, data from *L. ochroleuca* and *S. polyschides* must be considered with caution since they correspond to seaweed populations very distant from the Alboran Sea and the occurrence of different thermal ecotypes in their distribution areas is probable.

15.2.5 Inorganic Nutrients

There are no time series of inorganic nutrients in the area. However, they must be high due to the permanent cold, rich-nutrient upwelling in the kelp forests. It can be hypothesized that the perennial *L. ochroleuca* stores nutrients as other perennial kelps do (Mann 1973; Gagné and Mann 1981; see Chap. 4 by Gordillo). The nutrient storage strategy is very different in the annual *P. purpurascens* from the Strait of Gibraltar. The C:N and N:P ratios increased from spring (when recruitment of sporophytes took place) to summer (when the thalli reached the greatest size and the production of sori began), and they remained constant until the first storm period in the autumn when the sporophytes were detached. The ratios suggested that the growth of *P. purpurascens* could be limited by both N and P, but the time course of the C:N:P Redfield ratio (Redfield 1934; Atkinsons and Smith 1984) showed that the growth was P-limited (Flores-Moya et al. 1995).

P. purpurascens shows external carbonic anhydrase (CA) activity (see also Chap. 19 by Roleda and Hurd). This enzyme catalyzes the dehydration of HCO_3^- (the most abundant inorganic carbon species in seawater) to CO_2 which diffuses into the cells. However, under fast flowing water due to tidal currents the extracellular CA may be physically removed from the thallus surface (Flores-Moya and Fernández 1998).

15.3 Growth and Reproduction

An estimate of the mean age of *L. ochroleuca* individuals of about 4–6 m length collected at 45 m depth at Alboran Island (assuming one annual cycle per pair of bands formed by the meristoderm; Klinger and DeWreede 1988) resulted in an age of 8–11 years (Flores-Moya, unpublished data). Similar age structure was found in the populations growing at 60 m depth in the Strait of Messina (Drew 1972). *S. polyschides* and both species of *Phyllariopsis* can be considered as “monocarpic” (the term used for flowering plants which die after setting fruit) since the thalli become senescent after sorus formation. The basic difference between the two genera is that the *S. polyschide*s thalli sometimes do not become fertile during the first year (i.e., they could be considered biennial) whereas growth and reproduction in *Phyllariopsis* occurs in less than 1 year (Flores-Moya et al. 1993). The thalli are recruited in spring and are detached from the substratum in autumn–winter.

L. ochroleuca bears sori all year long but the highest percentage of fertile blades occurs in the spring and summer. The optimal temperature range for both zoospore germination and growth of gametophytes is 15–18°C (Table 15.1); gametogenesis is inhibited at temperatures below 10°C. Growth of young sporophytes is maximal at irradiances of 20–40 µmol photons m^{-2} s^{-1} (Izquierdo et al. 2002). *S. polyschides* and both species in *Phyllariopsis* become fertile in summer (Flores-Moya et al. 1993). Gametophytes of both species of *Phyllariopsis* are dioecious but unusually monomorphic (Henry 1987; Flores-Moya and Henry 1998). Thermal limits for growth and reproduction for *Phyllariopsis* gametophytes range from 10 to 20°C (Table 15.1).

15.4 Productivity

There are no data on net primary productivity of *L. ochroleuca* or *S. polyschides* in the Alboran Sea or the Strait of Gibraltar. The measurements for populations of *L. ochroleuca* from the shallower sublittoral of NW Spain ranged from 1 to 2 kg C year^{-1} m^{-2} sea bottom (Fernández and Niell 1981). These figures were similar to those found in other species of *Laminaria* (Mann 1982; Sjøtun et al. 1995) but lower than those found in *Laminaria hyperborea* growing at depths lower than 30 m in Norway (3 kg C year^{-1} m^{-2} sea bottom; Abdullah and Fredriksen 2004). The net primary productivity of *S. polyschides* from North Spain ranged from 0.5 to 1 kg C year^{-1} m^{-2} sea bottom (Fernández and Niell 1981). The net annual primary productivity measured in *P. purpurascens* growing at 30–35 m depth in the Strait of Gibraltar was approximately 50 g C year^{-1} m^{-2} sea bottom, a very low value in comparison to the values found in other kelps (Flores-Moya et al. 1993). This result was later interpreted as a consequence of the P-limited (Flores-Moya et al. 1995) and irradiance-limited (Flores-Moya et al. 1996, 1997; Flores-Moya 1997) growth.

15.5 The Communities of Kelp Forests in the Alboran Sea and the Strait of Gibraltar

The best-known kelp forests considered here are located on the sea bottom at Alboran Island (Templado et al. 2006). *S. polyschides* forests range from 15 to 35 m depth, with a maximum density of 5–8 thalli m^{-2} sea bottom. Between 25 and 50–60 m depth, the kelp forest is formed by *L. ochroleuca*, with densities of 2–4 thalli m^{-2}. Both species form a continuous canopy due to the more or less horizontal position of the blades. In the case of *L. ochroleuca* forests, new individuals are recruited after a catastrophic event causing the loss of old thalli; in fact, young thalli only appear in cleared areas. The intraspecific competition is much more intense in the very deep water kelp beds of *P. purpurascens*. The irradiance level below one blade at 30 m depth was lower than the photosynthetic irradiance-compensation point. This could explain two facts. On the one hand, the overdispersed distribution of thalli on the sea bottom which avoided the overlapping of blades (Flores-Moya 1997). On the other hand, the growth of sporophytes which occurred only after the detaching of some individuals (Flores-Moya et al. 1996, 1997) following a defined self-thinning pattern (Fig. 15.4).

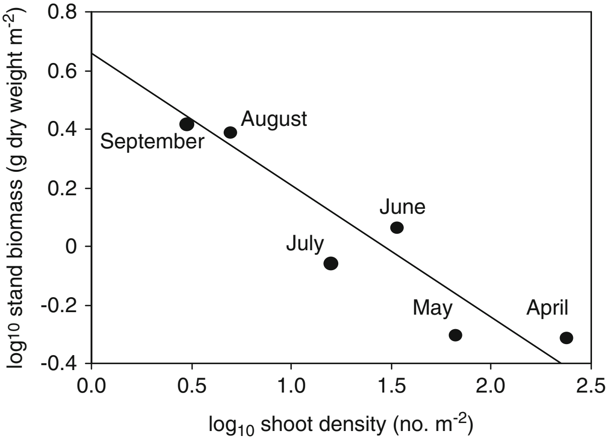

Fig. 15.4 Relationship between $\log_{10}$ stand biomass and $\log_{10}$ shoot density along the life span of the sporophytes of *Phyllariopsis purpurascens* (from April to September) growing at 30 m depth in Tarifa (Strait of Gibraltar). A significant negative slope suggested the occurrence of self-thinning in this population (Flores-Moya et al. 1997)

Kelp forests are considered as one of the most productive and dynamic ecosystems on Earth (Mann 1973). Moreover, they have very high species richness. About 1,800 different species from different phyla find refuge or breed in the kelp forests in the United Kingdom (Birkett et al. 1998) and a total of 238 faunal species were recorded in the Norwegian *Laminaria hyperborea* forests (Christie et al. 2003, 2009). The species richness associated with the *L. ochroleuca* forests at Alboran Island (Templado et al. 2006) has been estimated to be around 1,800–2,000 species, although this island is minuscule (614 m maximum length and 300 m maximum width) in comparison to the British Isles or to the shoreline of Norway, and its shelf is not extensive due to the steep slopes. Thus, it could be hypothesized that the Alboran Island kelp forests may be the ecosystem with the highest biodiversity in Europe.

15.6 Conservation and Prospects

The conservation status of kelp forest in the Strait of Gibraltar and the Alboran Sea is satisfactory, principally due to the deep locations of these communities. The best conserved kelp forests are located on the sea bottoms of Alboran Island. The Natural Park of the Strait and the Marine and Fishing Reserve of Alboran Island are protected areas that help to preserve these singular deep water kelp forests. Recent observations with unmanned ROVs from the organization OCEANA (Aguilar et al. 2010) have contributed more knowledge about the extent, depth distribution, and organisms associated with the deep water kelp forests and kelp beds in the Strait of Gibraltar and in the Alboran Sea. The use of ROVs makes it possible to avoid the problems associated with deep water diving in areas with strong currents. However, our knowledge of functional ecology and trophic ecology of these communities is very sparse. This gap needs to be addressed in order to understand the contribution of kelp forests in the Strait of Gibraltar and the Alboran Sea to the nutrient cycles and productivity of higher trophic levels.

15.7 Concluding Remarks

Kelp forests are one of the most characteristic seaweed communities in temperate oceans. They receive a lot of attention due to their ecological roles, their commercial interests (i.e., as a source of alginates), or because they are the nursery and habitat of fishery species such as lobsters, crabs, and mollusks. However, the singular deep water kelp forests from the Strait of Gibraltar and the Alboran Sea long remained almost unknown to the phycological community. The structure of kelp forests and kelp beds, the species richness, and some autoecological topics have been addressed. However, ecological processes such as the role of nutrient cycles or their contribution to higher trophic levels remain unstudied.

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Chapter 16
Macroalgae in Tropical Marine Coastal Systems

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16.1 Introduction

Tropical marine environments are oligotrophic, warm, and expose primary producers to relatively high levels of photosynthetically active radiation (PAR) that penetrates as far as several hundred meters into the water column. Many tropical marine coastal communities are structurally dependent upon ecosystem engineering organisms such as seagrasses, mangroves, and corals in which the role of macroalgae is fundamentally different from temperate marine systems. This chapter will begin with a brief overview of the abiotic conditions, such as temperature, light, and nutrients, which have a defining influence on algal diversity, distribution, and dynamics with particular emphasis given to coral reef habitats because of the extensive body of research focused on this ecosystem. This will be followed by more detailed information on the role of macroalgae in the three main tropical marine ecosystems. Although they are not the main habitat providers in

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tropical coastal areas, macroalgae are essential to the productivity, structure, and function of each of these communities. Throughout this chapter, the role of macroalgae in regime shifts from systems dominated by the aforementioned habitat providers to ones dominated by algae as well as the factors that bring about these changes will be discussed.

16.2 Abiotic Conditions

Compared to the extreme seasonal changes in temperate regions, the variability of abiotic conditions in the tropical zone is limited, aside from the influence of the rainy season which can reduce salinity, increase water velocity, and decrease PAR.

16.2.1 Temperature

Three types of physiological responses to temperatures determine a species' biogeographical boundaries (Breeman 1988): growth, reproduction, and mortality (see Chap. 3 by Eggert). Pakker et al. (1995) suggested that tropical macroalgae are the most stenothermal macroalgae of any biogeographical region; their growth generally reaching a peak between 25 and 30°C, with those restricted to the tropical western Atlantic surviving a total variation of only 10/13°C. In comparison, macroalgae from colder regions are tolerant of a much wider range of temperatures (see Chap. 3 by Eggert and Chap. 18 by Bartsch et al.). Macroalgae of the tropical to warm-temperate Eastern Atlantic Ocean and Mediterranean Sea show the same temperature limitations as those of the Western tropical Atlantic Ocean and Caribbean Sea. Unsurprisingly, species restricted to the subtidal regions, and thus rarely exposed to extreme variations in abiotic conditions, are least tolerant of high temperatures, generally succumbing to temperatures exceeding 33°C. Furthermore, both subtidal and intertidal species appear to be limited by temperatures lower than 18/20°C.

16.2.2 Nutrients

Seawater in tropical regions is generally low in nutrients due to strong stratification of the water column that prevents vertical mixing of nutrients. Tropical marine habitats that are not exposed to terrestrial effluents are particularly nutrient poor, thereby preventing the proliferation of phytoplankton and macroalgae and increasing the light availability for benthic organisms. Occasionally nutrients become temporarily available through terrestrial runoff during the rainy season or upwelling events, encouraging strong seasonal responses (see also Chap. 21 by Teichberg et al.). After several decades of scientific research it has become clear that nutrients are cycled tightly within tropical ecosystems to prevent losses and enable a high level of productivity. The higher light levels and temperatures of the tropics make continuous productivity possible despite lower nutrient concentrations.

The increased supply of nutrients to the marine environment, resulting from human activities (agriculture, development, sewage, etc.), has been linked to increased algal growth in environments where they were previously a limiting factor (see below). However, the concentration of nutrients in seawater is not always directly related to macroalgal growth rates. For example, under low ambient nutrient conditions, high water motion can also stimulate increased growth rates of macroalgae (McCook 1999). Tropical macroalgae are very efficient nutrient users that are capable of taking advantage of nutrient pulses through surge uptake mechanisms. Additionally, they can store and recycle nutrients in their tissues for extended periods of time (Fong et al. 2003). In tropical macroalgae, small increases in nutrient concentrations can trigger an uptake response comparable to that of bloom-forming species from temperate estuaries responding to much higher nutrient concentrations (Kennison 2008; Fong et al. 2001, 2003). The concept that nitrogen and phosphorus are limiting nutrients in the tropical environment remains a source of controversy (Bell 1992; Lapointe 1997; Bell et al. 2007). Results of nutrient-enrichment experiments using macroalgae taken from coral reef and seagrass habitats indicate that nitrogen limitation is common (e.g., Lapointe et al. 1987; Littler et al. 1991; McGlathery et al. 1992; Delgado and Lapointe 1994; Collado-Vides et al. 2007). Several investigations have reached the same conclusion that phosphorus availability limits the productivity of fleshy macroalgae in oligotrophic reef waters (Lapointe et al. 1987, 1992; Littler et al. 1991). However, alkaline phosphatase activity (APA) enables some macroalgae to fulfill their phosphorus requirements by facilitating the utilization of organic phosphorus. These mechanisms have been well documented in macroalgae growing in the inshore regions of the Great Barrier Reef (GBR) where nutrient supply can be extremely variable and dependent on inshore human activities (Schaffelke 2001).

16.2.3 Light

Light is the most important physical factor affecting primary productivity in the marine realm. At low latitudes, light levels and water transparency are high due to limited suspended sediments, particulate and dissolved organic matter, and phytoplankton. Additionally, very little PAR is lost due to limited scattering and reflection of light on the sea surface. Although light penetrates deeper in the water column in the tropics than in temperate regions, light attenuation with depth still creates a gradient of light quantity and quality (see also Chap. 1 by Hanelt and Figueroa). Light in this way plays a structuring role in the distribution of tropical macroalgae. Rhodophytes, like crustose coralline algae, are common throughout all reef zones, from the intertidal to 80–90°m deep, where the light intensity has been estimated at ~0.2% of the surface radiation (Van den Hoek et al. 1978), and even as deep as 268 m in the Bahamas (Littler et al. 1985, 1986). On Curaçao sparse algal turfs reach their lower limit around 65 m, where PAR levels are as low as 1% of that found at the surface (Van den Hoek et al. 1978). Green macroalgae generally are most common in shallow waters, but have been found forming entire communities consisting of *Udotea, Caulerpa*, and *Halimeda* species at depths of 25 m on Saba Bank (Lesser Netherlands Antilles) (Littler et al. 2010a) as well as *Johnson-sealinkia profunda* colonies found at the extreme depth of 200 m in the Bahamas (Littler and Littler 1988). In addition, the lack of a conspicuous seasonal cycle in photoperiod in the tropics compared to mid and high latitudes provides a relatively constant supply of PAR throughout the year.

Although ultraviolet radiation (UVR) levels are high in the tropics, studies focused on its impact on macroalgae have for the most part been limited to polar and temperate seaweeds due to ozone depletion in these regions (Bischof et al. 2006; see also Chap. 20 by Bischof and Steinhoff). Recently, Figueroa et al. (2009) showed that seaweeds from the Red Sea show dynamic photoinhibition as an efficient mechanism of acclimation to high PAR as well as UV irradiance levels. This is not unique to tropical seaweeds but has been shown for other seaweeds in high light exposed environments (Figueroa et al. 1997). A recent investigation of tropical marine macroalgae collected from Belize at depths of 0.3–26 m depths showed that UVR caused an additional decrease of photosynthetic performance during high light stress which varied according to species, depth of growth, and UV penetration at the site of collection (Hanelt and Roleda 2009; see also Chap. 1 by Hanelt and Figueroa). However, this same study also provided evidence that UVB radiation may not only cause negative effects on cellular processes of seaweeds but may also support recovery processes in high UVR adapted seaweeds (Hanelt and Roleda 2009).

16.3 Vegetation Structure

16.3.1 Succession

Succession patterns depend on the characteristics of vacant space, bottom-up availability of nutrients, and top-down grazing characteristics. Many studies have documented the recovery of coral reef systems after storms and hurricanes and the succession of algae during this process as well as the experimental succession on settlement plates. In general, there is first a dominance of simple turf like green and brown filamentous seaweeds, a midsuccessional stage with thin and finely branched red filamentous seaweeds, and a late stage dominated by coarsely branched and thick canopy-forming seaweeds. The 37-year history of the Tiahura Outer Reef Sector (Moorea) constitutes one of the longest records of coral reef dynamics (Adjeroud et al. 2009). Between 1991 and 1994, the decline in coral cover was accompanied by colonization by turf algae (16.2 ± 5.5% in 1991 to 48.5 ± 2.5%

in 1994). However, instead of a successional sequence of algal growth towards the proliferation of canopy-forming macroalgae, the cover of algal turf decreased after 1994, and returned to the predisturbance levels within a decade (Adjeroud et al. 2009). These results suggest that the availability of vacant space was not sufficient to cause a persistent increase in algal cover, and that other factors, such as a reduction in grazing pressure or an increase in nutrients, may be necessary for a regime shift to macroalgal dominance (McManus and Polsenberg 2006; Mumby 2009; see also Chap. 21 by Teichberg et al.). A similar story emerged from the protracted loss of coral cover in Jamaica following two hurricanes, three bleaching events, a reduction of grazing pressure (overfishing and disease), and a potential pulse of nutrients which all contributed to a dramatic increase of algal cover, from ~4% in 1977 to ~92% in 1993 (Hughes 1994). Experimental studies, like that of Hixon and Brostoff (1996), demonstrate the importance of herbivores on the successional trajectory in tropical marine ecosystems. In conclusion, the impacts that macroalgae can have on tropical marine communities are complex and are dependent upon the identity of the herbivores present as well as the developmental stage of the seaweed community (see Coral reefs below).

16.3.2 Diversity

Tropical marine ecosystems are among the most diverse ecosystems on our planet. While invertebrates have received a great deal of attention during biodiversity surveys and studies in the past, macroalgae have received much less consideration. Some early studies that have assessed macroalgal diversity patterns across latitudinal gradients have arrived at conflicting conclusions, finding high species diversity at low and midlatitudes as well as decreasing diversity towards lower latitudes (e.g., Pielou 1977; Santelices and Marquet 1998). A more recent literature review by Kerswell (2006) revealed distinct gradients in species and genus diversity worldwide. When all macroalgal genera were considered, tropical regions had lower diversity than temperate regions. Only when a more reef associated order like the Bryopsidales was examined, diversity peaked at low latitudes. Furthermore, Konar et al. (2010) confirmed the common trend of higher taxa diversity at midlatitudes compared to low latitudes in the northern hemisphere, particularly in the intertidal.

Until recently, the coral reef seaweed hotspots of the Caribbean Sea were considered to be at Diamond Rock in Martinique and the Pelican Cays in Belize. However, on a recent expedition to the Saba Bank, Littler et al. (2010a) collected between 150 and 200 seaweed species from 17 different dive sites, demonstrating that there is still much to discover. Their checklist of 98 taxa including 43 Rhodophyta, 26 Chlorophyta, 26 Phaeophyceae (Heterokontophyta), and three Cyanophyta contained several unknown species as well as some previously unrecorded seaweed communities. These communities were located at depths of 25–30 m and were dominated by green, brown, or fleshy red macroalgae. In contrast to the predominant idea that abundant macroalgae indicate compromised reef health, no indications were found that conflicted with the existing definition of "pristine" oligotrophic reef systems (Littler et al. 2010a).

Turf algal assemblages can provide the majority of the primary productivity on a coral reef (Adey and Steneck 1985; Fricke et al. 2011). These assemblages are multispecies associations, characterized by undifferentiated upright axes and a rapid turnover (Carpenter et al. 1985). Although inconspicuous, they occur almost everywhere on reefs where space is available (Littler and Littler 1984; Steneck and Dethier 1994). Although they are fast growing, fleshy macroalgae often outcompete with them for limited light and space (Hay 1981). Algal turfs are able to persist under intense herbivory and physical stress in areas where other algae are continuously excluded. Their high productivity rather than their standing crop maintains the high standing stocks of grazers characteristic of coral reefs (Hatcher 1988; Carpenter 1986; McCook et al. 2001). In deep and shallow reef zones, where grazing pressure is low, frondose algae rather than turfs commonly dominate (Van den Hoek et al. 1978; Vuki and Price 1994).

Crustose coralline algae (CCA) play three important roles on coral reefs: (1) limestone formation, (2) the consolidation of loose substrates (Fabricius and Dea'th 2001), and (3) primary production (Littler and Littler 1984). In shallow waters they can build massive carbonate structures on reef crests despite the typically turbulent conditions (Adey and Vassar 1975). Due to their unpalatable nature, coralline algae are more resistant to grazing and therefore survive well in areas where grazing intensity is high.

Fleshy frondose macroalgae are mainly composed of tropical fucoids like *Sargassum*, *Turbinaria*, and *Cystoseira*. They often dominate on shallow reef flats and crests of inner reefs or in deeper fore reef zones and are generally absent from mid and outer shelf reefs (Vuki and Price 1994; McCook 1996). *Sargassum* species are often dominant in terms of biomass and canopy cover, due in part to their high productivity (Vuki and Price 1994; McCook 1996; Schaffelke and Klumpp 1997). Foliose macroalgae are seasonal opportunists and can be found in areas less dominated by canopy-forming macroalgae (Schaffelke and Klumpp 1997). Due to high biomass turnover, reefs with a high cover of large Phaeophyta are often regarded as detritus-driven ecosystems (Schaffelke and Klumpp 1997).

16.3.3 Zonation

The zonation and distribution of macroalgae is highly variable, which complicates extrapolations between similar habitats and across habitat types within regions and between different parts of the world. The distribution and zonation of macroalgae is strongly dependent on the structure of the habitats which is formed by historical (geology: reef types), abiotic (nutrients, temperature, and light), and biotic (grazing and competition) conditions (Berner 1990). We therefore describe the zonation using examples from a Caribbean fringing reef, a Pacific Atoll, and a Barrier reef.

On Curaçao in the Caribbean, van den Hoek et al. (1978) described the vertical distribution of reef macroalgae and distinguished seven different algal communities. The narrow eulittoral zone is inhabited by cyanophytes, turfs, and smaller macroalgae. In the top part of the surf area, the seaweed community is composed of *Ulva* and the brown seaweeds *Giffordia duchassaigniana* and *Sphacelaria tribuloides*, whereas in the deeper part the brown seaweed *Sargassum polyceratium* and the red algae *Hypnea musciformis* and *Laurencia* spp. dominate. In the sublittoral zone on the platform, from the surf area down to 3 m deep is a shallow reef occupied by coral rubble fragments aggregated by the crustose red alga *Porolithon pachydermum* and macroalgal turfs. The foliose brown seaweed *Lobophora variegata* forms a girdle-like vegetation at 30–38 m deep and the erect *Sargassum polyceratium* occurs from 15 to more than 65 m depth. Many shade adapted species are present in this zone reaching to depths of 55–65 m, including the green macroalgae *Udotea* and *Caulerpa* species and numerous red algae. Crustose red algae reach into the deep where the reef terminates and a sandy plateau forms at a depth of 75–90 m.

Womersley and Bailey (1969) described the zonation of macroalgae in the Solomon Islands on four types of coral reefs, with differences in hydrodynamic activity. The seaward rim consists of crustose coralline algae, mainly *Lithophyllum* and corals, and behind this the coralline alga *Porolithon onkodes* dominates. On shallow intertidal rubble near the island shore, crustose and endolithic green algae and cyanobacteria dominate.

Studies of the algal assemblages on the GBR have shown marked latitudinal, cross-shelf, and within-reef variations in composition and abundance (Wismer et al. 2009). In contrast to midshelf and outer-shelf reefs, inshore or coastal reefs typically have abundant and conspicuous macroalgal communities (Diaz-Pulido et al. 2007). The reef flat zone in particular is often dominated by dense and highly productive beds of large fleshy brown macroalgae, predominantly *Sargassum* (e.g., McCook 1997; Schaffelke and Klumpp 1997).

16.3.4 Seasonal Dynamics

Varying weather conditions throughout the year have a strong influence on the abundance of macroalgae in tropical regions. In particular, lower temperatures and the influx of nutrient-rich freshwater during the rainy season can cause a significant increase of algal biomass. For example, in Kenya epiphyte coverage on seagrasses can double or triple during the shift from the NE monsoon (warm temperatures, less rain, and light winds) to the SE monsoon (cool temperatures, heavy rains, and strong winds) (Uku and Björk 2005). In Florida, researchers observed an increase of epiphyte biomass during the rainy season so extreme that it became three times greater than seagrass blade biomass (Lapointe et al. 2004). Of course, the hurricane/cyclone season presents potential for extreme events in the tropical marine environment each year as well. It is widely recognized that these events characterized by intense water velocities, higher freshwater input, and mechanical disturbance can both disrupt and maintain the balance between macroalgae and seagrass, mangrove, and coral reef communities.

Macroalgae within coral reef habitats display a great amount of seasonality as well (Coles and Fadlalah 1991). A very comprehensive overview of seasonality of four major functional groups: canopy, foliose, turf, and CCA was accomplished by Aterweberhan et al. (2006). They monitored biomass of all these groups in four reef zones at two localities in the southern Red Sea. All functional groups showed seasonal variation in biomass, although seasonal variation differed among groups and reef zones. Canopy and foliose macroalgae were highly seasonal, whereas turf algae and crustose corallines showed much less seasonal variability. The biomass variation of *Sargassum* spp. greatly determined the seasonal variation of standing biomass of all algal types on the shallow inner and middle reef flats. On the deeper, outer reef flat, *Turbinaria triquetra* contributed most to the seasonal variation. Foliose algae contribute most to the seasonal variation only where canopy-forming macroalgae were lacking, like on the middle reef flat. Crustose corallines and turf algae only contribute considerably to the total biomass during the hot season when macroalgae are strongly reduced. On the fore reef, crustose corallines contribute most to the biomass throughout the year. In general, turf algae contributed least to the standing biomass during all seasons, at all sites, and all reef zones.

16.4 Macroalgae and Their Roles and Interactions in the Three Main Tropical Ecosystems

16.4.1 Macroalgae and Coral Reef Interactions

16.4.1.1 Herbivory

Herbivory is widely recognized as the main driver affecting the distribution and abundance of macroalgae on tropical coral reefs (Carpenter 1986; Hay 1997; Hughes et al. 2007; Burkepile and Hay 2010). Several experimental studies have demonstrated that coral reef herbivores can remove up to 100% of daily algal production in some coral reef habitats (Duffy and Hay 1990; Hughes et al. 2007). In tropical marine habitats, herbivorous fish and sea urchins are the dominant grazers of macroalgae (Williams et al. 2001; Mumby et al. 2006; Burkepile and Hay 2010). Sparisomid parrotfishes represent more than 80% of the herbivorous fish biomass that is dominant in Caribbean reefs, along with the acanthurids (surgeonfishes, tangs, and unicornfish), kyphosids (sea chubs), and pomacentrids (damselfishes) (Mumby 2009). Herbivorous fish feed on an array of algal types, including fleshy macroalgae, algal turfs, and encrusting coralline algae (Hay 1997; Mumby 2009). Algal turfs are easily digested and have a high energetic and protein value relative to other macroalgae and are thus the preferred food of many herbivorous fish, in both the Caribbean Sea and other tropical habitats (Bruggemann et al. 1994; Kopp et al. 2010). Based on their experiments in the Caribbean (Guadaloupe), Kopp et al. (2010) determined that *Acanthurus coeruleus* (Blue tangs) and *Sparisoma aurofrenatum* (Redband parrotfish) graze preferentially on algal turfs, while *Sparisoma rubripinne (Redfin parrotfish)* and *Sparisoma viride* (Stoplight parrotfish) are more inclined towards *Halimeda* spp. while *Acanthurus bahianus* (Ocean surgeon) prefer Phaeophytes. Their results also revealed the aversion of herbivorous fish towards *Dictyota* spp., a brown macroalgae that uses chemical compounds as a grazing deterrent (Hay 1997; Paul et al. 1990). On the GBR, Mantyka and Bellwood (2007a) report that grazers of macroalgae on the reef crest of Pioneer Bay are composed of six reef fish species (two rabbitfishes, three parrotfishes, and one damselfish) which display species-specific feeding behavior. For example, the rabbitfishes, *Siganus doliatus* feed heavily on *Hypnea* spp. while *Siganus canaliculatus* feed intensively on *Sargassum,* and the three parrotfishes *Chlorurus microrhinos*, *Hipposcarus longiceps,* and *Scarus rivulatus* were the dominant grazers of calcified *Halimeda* spp. (*H. cylindracea*, *H. discoidea*, *H. opuntia)*, and *Amphiroa* spp. During their experiment, *Chlorodesmis fastigiata* and *Galaxaura* spp. were least affected by herbivory, suggesting a reduced palatability owing to their chemical deterrence and calcareous structures (Paul et al. 1990). More recently, Cvitanovic and Bellwood (2009) have reported that the dominance of herbivorous fish over macroalgae species and specific reef areas can show local variability. In an experiment conducted on the Orpheus Islands, they found similar rates of macroalgae removal in three separate bays; however, three different species of herbivores were responsible for the grazing control. They also found that *Kyphosus vaigiensis* (Brassy chub) were responsible for high rates of removal of *Sargassum* spp., although past studies had identified *Siganus canaliculatus* (White spotted spinefoot) and *Platax pinnatus* (Dusky batfish) as the dominant grazers of *Sargassum* spp. in Pioneers Bay *(*Mantyka and Bellwood 2007b). Most recent studies highlight the importance of herbivore richness and diversity (Burkepile and Hay 2010) as well as abundance and biomass (Mumby et al. 2006; Kopp et al. 2010) in maintaining reef macroalgae community structure, reducing fleshy macroalgal blooms and enhancing coral reef recovery and resilience. For example, Burkepile and Hay (2010) determined that complementarity feeding among fish species not only impacted structure of macroalgal communities, but also enhanced coral survivorship and growth on reefs in the Caribbean Sea (Florida Keys, USA). The authors observed that fast grazing by ocean surgeonfish (*Acanthurus bahianus*) and princess parrotfish (*Scarus taeniopterus*) kept macroalgae communities dominated by short, filamentous algae and crustose coralline algae, both algal states that do not suppress coral growth. Conversely, within the established benthic communities, the authors observed that the redband parrotfish (*Sparisoma aurofrenatum*) played a vital role in the removal of upright macroalgae cover which can be detrimental for coral growth and survival. To further investigate the role of herbivory on regulation of macroalgae community structure, numerous herbivory exclusion experiments have been conducted in tropical coral reefs (Lirman 2001; Hughes et al. 2007; Smith et al. 2010a; Hoey and Bellwood 2010). These studies provide evidence of how exclusion of large herbivores is followed by undesirable blooms of upright macroalgal species, which are considered less susceptible to herbivory and capable of causing phase shifts from coral to macroalgae dominated systems. Mork et al. (2009) conducted a 6-week herbivore exclusion study on a moderately disturbed coral reef on the Kenyan coast. Their results show a 77% increase of algal biomass, largely attributed to a 1,000% increase in corticated forms of algae, dominated by *Dictyota* spp. Sotka and Hay (2009) reported similar results from an experiment conducted in the Florida Keys. After 142 days of monitoring, they observed that coral slabs exposed to natural densities of large herbivorous fishes were dominated by crustose coralline algae, short (<0.5 cm) filamentous turf algae, and upright macrophytes, which never exceeded 15% cover. In contrast, herbivore exclusion treatments were subject to 80–100% upright macroalgae cover.

The role of herbivory in regulating macroalgal communities can be severely compromised in overfished and degraded reefs and may result in phase shifts from coral to algae dominated systems (Mumby et al. 2006). In areas suffering from moderate levels of overfishing, a lack of top predators can stimulate an increase of herbivore biomass. However, in severely overfished areas, herbivorous fish are not able to control macroalgae because they too become subject to overfishing and are unable to become sufficiently large in size to regulate algal production, even if they are numerically abundant (Kopp et al. 2010). A significant reduction of fishing pressure of herbivorous fish (Mumby and Harborne 2010) as well as a reduction of confounding disturbances such as nutrient pollution (Smith et al. 2010a) has been suggested as a means of reversing algal phase shifts.

16.4.1.2 Chemical Defenses

Macroalgae defend against herbivory using a number of strategies, including morphological, structural, and chemical defenses as well as associations with other algae or benthic organisms (Hay 1997; Paul and Puglisi 2004; Amsler 2008; Smith et al. 2010b; Fong and Paul 2011; see Chap. 9 by Amsler). Morphological and structural defenses include calcification and toughness, which are characteristics of the *Halimeda, Dictyota,* and *Lobophora* genera (Paul et al. 2001). These species are coarsely branched, leathery, or rubbery and have hard calcium carbonate tissues which are of little interest or nutritional value for herbivores (Schupp and Paul 1994; Hay 1997). Some macroalgae utilize secondary metabolites to help protect against pathogens, fouling organisms, and herbivores (Fong and Paul 2011). A significant quantity of natural products has been extracted and isolated from tropical marine green, red, and brown macroalgae, of which halides like bromine and chloride are very common as well as compounds like terpenoids (Fong and Paul 2011). Chemical deterrents in calcified green algae from the genera *Caulerpa* and *Halimeda* have been well studied and experiments have shown that their chemical composition deters both parrotfishes and sea urchins alike (Schupp and Paul 1994). Brown algae are known to utilize polyphetanolic compounds as deterrents along with terpenoids, which are commonly present in the order Dictyotales (Pereira and Da Gama 2008). Red macroalgae possess a great variety of secondary metabolites and the genus *Laurencia* has been widely studied for this reason (Blunt et al. 2007).

The study of chemical defenses of macroalgae has been widely investigated for over two decades and most of the research has been focused on their utilization against grazers (fishes, sea urchins, and gastropods) and their effect on coral species. For example, from their experiments conducted in the Caribbean and tropical Pacific, Rasher and Hay (2010) provide evidence that five of seven seaweeds (71%) caused bleaching of the coral species *Porites porites* in Panama. While in Fiji, three of eight species (38%) caused bleaching of *Porites cylindrica*. Seaweeds were observed to damage corals via abrasion, shading, or lipid-soluble allelopathic compounds transferred through direct contact. The effects of a lipid-soluble extract from various species of macroalgae (*Ochtodes secundaramea, Dictyota bartayresiana, Lobophora variegata, Halimeda opuntia, and Amphiroa fragillisima* in Panama) caused significant coral bleaching and suppression of photosynthetic efficiency in assays using both intact seaweeds and chemical extracts. The two species that did not cause bleaching in any of the two assays were *Padina perindusiata* and *Sargassum* spp. These results illustrate how overfishing of herbivorous fish, capable of suppressing undesirable macroalgae, will inevitably result in an increase of direct coral–algae contacts and further impair corals through allelopathic interactions. Major gaps still persist concerning the ecological role that macroalgal secondary metabolites play apart from feeding deterrence (Pereira and Da Gama 2008).

16.4.1.3 Providers of Spatial Refuge

Persistence of unpalatable macroalgae on coral reefs can be facilitated by spatial refuges and associational assemblages. An associational refuge is one in which a host species provides protection that enhances the survival of associate species (Bittick et al. 2010). These interactions are becoming increasingly recognized as important drivers of ecosystem function. Smith et al. (2010b) have found that patches of the green algae *Caulerpa sertularioides* found in reef areas of Uva Island in Panama can persist due to their association with an epiphytic cyanobacterium (*Lyngbya majuscula*). The cyanobacterial epiphytes on *C. sertularioides* thalli provide protection from herbivory for both upright assimilators and stolons. Similarly, associational defenses provided by cyanobacteria have been reported to be responsible for the 5-year persistence of the highly palatable alga *Acanthophora spicifera* on the Uva Island reef (Fong et al. 2006). On the coral reefs of Moorea, French Polynesia, Bittick et al. (2010) observed that aggregations of the brown macroalga *Turbinaria ornata* provide mechanical and chemical refuge from herbivory to associated macroalgae. The study showed that aggregations of *Turbinaria* significantly enhanced species richness, especially of fleshy species like *Caulerpa serrulata*, *Dictyota bartayresiana, Sargassum mangarevense, Valonia utricularis,* and *Ventricaria ventricosa.* On the contrary, in coral heads without *Turbinaria,* there was less algal density and these were dominated by crustose coralline algae, filamentous algal turfs, and cyanobacteria. As a result, unprotected coral heads without *Turbinaria* had the lowest diversity of all treatments.

16.4.1.4 Nutrient Enrichment

The influence of excess nutrient supply on the development of reef macroalgae is a topic of major debate between marine researchers (Littler and Littler 2006; Mork et al. 2009; Smith et al. 2010a). Experimental studies have often investigated the effect of nutrient enrichment in the presence and absence of herbivory to determine its role in regulation of macroalgal growth and cover in tropical habitats, especially coral reefs. The available literature is divided between studies that report a significant effect of nutrient enrichment on enhancing growth and abundance of fleshy macroalgae and cyanobacteria in coral reef habitats and others that report no significant effect. For example, Littler et al. (2010b) conducted a 12-month study in a sedimentary lagoon at Carrie Bay Cay in Belize's barrier reef to compare the enrichment effects of dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) additions on algal community development. They found that SRP and SRP + DIN treatments stimulated the growth of cyanobacteria (*Spirulina* spp.) and inhibited settlement and colonization of CCA. Meanwhile, the DIN enrichments increased CCA cover, decreased cyanobacteria cover, and had no influence on fleshy macroalgae. Sotka and Hay (2009) reported similar findings related to fleshy macroalgae from a 20-week nutrient-enrichment experiment conducted in the shallow fore reefs of the Florida Keys. They concluded that herbivory is stronger than nutrient abundance in regulating macroalgae abundance and composition on coral reefs. Their results revealed that large herbivorous fish selectively grazed on nutrient-enriched macroalgae. On the contrary, experiments conducted by Smith et al. (2010a) on the reef slope at Puako Reef, Hawai'i found that both fertilization and herbivory exclusion impacted macroalgae community structure at different temporal scales. They observed that reducing herbivory led to rapid changes in benthic communities (1 month), while the effects of nutrient enrichment were only visible after 3–4 months. This can explain the lack of strong nutrient-enrichment effects noted in other studies, as they may be a result of short-term experiments. Vermeij et al. (2010) conducted experiments in Curaçao, Netherlands Antilles, to examine the effects of Caribbean turf algae on neighboring corals and interactions of these algae with nutrient enrichment and grazing. They found that nutrient enrichment significantly enhanced the capacity of turf algae to overgrow the coral *Montrastrea annularis*, since turf algae is also able to overgrow coral at ambient nutrient concentrations when herbivory is excluded or reduced.

16.4.1.5 Competition

Competition is an important force influencing the structure of coral reef communities and its effects can impact all stages of a coral colony's life cycle (Lirman 2001; Nugues and Bak 2006; Foster et al. 2008; Ritson-Williams et al. 2010; Vermeij et al. 2011). Macroalgae are known to compete with corals using different strategies which include the occupation of settlement substrate (Birrell et al. 2005; Vermeij 2006), physical disturbance (e.g., abrasion, shading, smothering) (McCook et al. 2001; Box and Mumby 2007), allelopathy (Gross et al. 2003; Kuffner et al. 2006; Foster et al. 2008), and direct transmission of pathogenic microbes (Vermeij et al. 2009). This competitive interaction is often species specific and capable of causing different levels of stress on coral species, potentially leading to coral mortality (Jompa and McCook 2002, 2003). In the Caribbean, Box and Mumby (2007) determined that *Lobophora variegata* and *Dictyota pulchella* inhibited coral growth on juvenile *Agaricia* spp. and *L. variegata* through shading and abrasion. In Hawaii, Vermeij et al. (2009) found that algal-induced microbes can cause mortality of the planular larvae of *Montipora capitata*. This effect on corals may be related to the ability of some algae to exude organic compounds that enhance rapid microbial growth, causing hypoxia and the reduction of larval resistance via the hampering of the coral's defense mechanisms against opportunistic microbes.

Although competition between macroalgae and corals has received significant attention from marine researchers, more evidence is still required in order to determine if algal growth is a cause rather than a consequence of coral mortality (McCook et al. 2001). More information is also needed concerning the interaction between coral larvae, macroalgae, and microbes in order to improve reef restoration techniques (Vermeij et al. 2009).

16.4.1.6 Facilitation of Coral Recruitment

CCA have been identified as facilitators of settlement and metamorphosis of a variety of marine invertebrate larvae as well as coral larvae (Ritson-Williams et al. 2010; Vermeij et al. 2011). CCA and coral interactions are known to be species specific, since corals have displayed different degrees of specificity in their requirement for CCA to induce successful settlement and metamorphosis. For example, an experiment conducted in the Caribbean (Belize) revealed that both *Acropora palmata* and *Acropora cervicornis* have higher rates of metamorphosis on the top surfaces of the CCA species *Hydrolithon boergesenii* and/or *Titanoderma prototypum* than on *Porolithon pachydermum (*Ritson-Williams et al. 2010). Further observations in the field (after 6 weeks) showed 15% survival of transplanted *A. palmata* recruits on both *T. prototypum* and *H. boergesenii*, and only 13% of A. *cervicornis* recruits on *T. prototypum*. These results suggest that CCA and settling coral polyp interactions can be species specific and also highlight the importance of benthic community composition for successful coral recruitment.

Aside from the positive role of CCA in coral recruitment, Vermeij et al. (2011) have reported that mixed communities of CCA (*Porolithon* spp. and *Hydrolithon* spp.) are capable of suppressing macroalgal growth and recruitment of the green macroalgae *Ulva fasciata,* based on studies conducted on a coral reef area in Hawai'i. Likewise, Birrell et al. (2005) have highlighted the negative impact of the association of macroalgal turfs and sediments have on coral recruitment of *Acropora millepora* found in the Orpheus Islands of the GBR. The results of that study indicated that sediment addition and algal turfs are capable of reducing coral settlement, although the effects of different algal turfs varied. In some cases, algal turfs inhibited coral settlement while other turfs inhibited settlement only when combined with sediments. Their results are suggestive of the need to study the impacts of similar associations to further understand the role of CCA in securing long-term resilience and recovery of coral reefs.

16.4.2 Macroalgae–Seagrass Interactions

In low nutrient environments, seagrasses and slow-growing macroalgae constitute a dominant regime in stable coastal waters. Seagrass habitats are important nurseries for commercially important fish species found within seagrasses and adjacent habitats such as coral reefs and mangroves (Dorenbosch et al. 2005). Within seagrass meadows macroalgae contribute to substrate complexity, act as a vital food resource for grazers, and have a significant influence on the cycling of nutrients. In nutrient-rich locations, macroalgal epiphytes are capable of achieving the same level of productivity as their seagrass hosts (Uku 2005). Some calcareous algae generate such immense quantities of $CaCO_3$ that entire beaches are constructed from the sand that they produce (Muzuka et al. 2005). However, enrichment of coastal waters can encourage the proliferation of algal blooms and initiate a breakdown in the balance of the system, resulting in decreased seagrass coverage (McGlathery 2001; Hauxwell et al. 2003; Lapointe et al. 2004). Macroalgae may provide short-term spatial heterogeneity and an enriched trophic resource, thereby appearing to be beneficial for invertebrate community diversity; however, they are often ephemeral and thus represent a threat to long-term biodiversity, relative to more permanent substrates, such as seagrasses (Cardosoa et al. 2004). Three distinct types of macroalgae (Epiphytic, Drift, and Calcareous Algae) have an important influence on the seagrass environment and thus dictate the structure of the following section.

16.4.2.1 Seagrass Epiphytes

In the tropics, epiphytic macroalgae are abundant and play a major ecological role in several habitats (see also Chap. 11 by Potin). In the Western Indian Ocean, macroalgal epiphytes constitute the most abundant group of epiphytes and can account for as much as 40% of the fresh weight of seagrass shoots (de la Torre-Castro et al. 2008; Uku and Björk 2001). In a Bahamas lagoon, the rates of net primary production (NPP) for seagrass epiphytes (5.2 ± 1.4 gC $kg^{-1}day^{-1}$) have been measured at approximately 40% of the NPP of the seagrasses themselves (Koch and Madden 2001). In highly enriched waters, it is not uncommon for seagrass-associated macroalgae to reach abundances higher than 0.5 kg m^{-2} and obtain canopy heights greater than 0.5 m (McGlathery 2001).

In Kenya, encrusting red coralline algae are the first to colonize seagrass leaves, establishing a purchase upon which subsequent epiphytes may settle, such as the green algae *Cladophora* spp. and red algae *Ceramium* spp. (Uku 2005). This succession of algal groups follows a consistent and predictable community gradient along the vertical length of seagrass leaves, which is likely determined by light exposure (Uku 2005). Of course, leaf colonization by epiphytes inevitably exacts a toll on the host. Dixon (2000) determined that epiphytes covering seagrass leaves can be responsible for reducing as much as 33.1% of available PAR. However, studies in the tropical waters of Eastern Africa provide evidence that shading by epiphytes has no effect on overall photosynthetic output of *Thalassodendron ciliatum* shoots (Uku 2005). It seems that *T. ciliatum* compensate for the lost PAR by maintaining photosynthetic activity in older epiphyte covered leaves while increasing the production of new leaves capable of higher photosynthetic activity.

In the presence of excessive nutrient concentrations, seagrasses may respond to smothering epiphytes by increasing their growth rate (Ferdie and Fourqurean 2004). Nutrient-enrichment studies have revealed decreased carbon reserves in the rhizomes of seagrasses in the presence of excessive concentrations of nitrate and ammonium (Invers et al. 2004). The unbalanced metabolism caused by this type of enrichment can result in a significant loss of nonstructural carbohydrates which allows seagrasses to persist during unfavorable conditions. Koch and Madden (2001) observed surge growth and *N*-storage in macroalgal seagrass epiphytes during enrichment studies, indicating an adaptive trait that allows for a competitive advantage when nutrients are limiting.

Epiphytes constitute an important food resource for seagrass herbivores and omnivores. In Zanzibar, the majority of commercially important fish species found within seagrass habitats, ranging from herbivores, piscivores, and invertebrate feeders, were found to graze directly on seagrasses and epiphytes (de la Torre-Castro et al. 2008). It seems that the higher nitrogen content of epiphytes and their resident invertebrates is an important supplement to nitrogen-poor seagrass diets. Various species of herbivorous parrotfish and surgeonfish collected from the seagrass beds of Curaçao were found to have diets consisting primarily of seagrass epiphytes (filamentous algae) and leaves (Nagelkerken and van der Velde 2004). From their work with manipulative studies in Florida, Baggett et al. (2010) suggest that increased grazing of epiphytes by herbivores (isopods, amphipods, gastropods, and caridean shrimps) compensates for increased coverage during nutrient-enrichment treatments. Recent studies in temperate seagrasses suggest that herbivorous invertebrates exert a strong top-down control of epiphytes on seagrasses (Moksnes et al. 2008). In fact, Spivak et al. (2009) found that the strongest effect during their nutrient-enrichment experiments was an increase in grazer biomass, not epiphytes, indicating an efficient transfer of nutrients through trophic levels. This evidence suggests that removal of large predators (tertiary consumers) is likely to cause trophic cascades, resulting in the increased severity and frequency of algal blooms in the seagrass environment.

16.4.3 Drift Algae Within Seagrass Meadows

In the tropics, drift algae can have a significant impact on the well-being of seagrass communities. Drift algae originate as epiphytes growing within seagrass meadows and neighboring habitats, having been liberated from the substrate during heightened hydrological disturbances. Accumulation of drift macroalgae within seagrass meadows is a function of water circulation characteristics determined by coastal physiography (Kopecky and Dunton 2006) and rates of entanglement in the seagrass canopy (Biber 2007). Transport of drift algae across the seabed is dependent upon substrate complexity, and in the case of seagrasses, it is determined by a meadow's patchiness, blade length, and shoot density. In shallow waters where water velocity is reduced drift algae can become entrained in bare patches. Algae also have a tendency to accumulate where wind or tidal generated water currents are sufficiently reduced to allow deposition out of the water column, be it on the leeward side of a bank or within a protected depression (Kopecky and Dunton 2006). Once entangled, drift algae can rapidly proliferate under favorable conditions generated by freshwater inputs, ideal temperatures, and nutrient loading (Biber 2007). In the Gulf of Mexico, drift macroalgae can reach a biomass exceeding that of the dominant seagrass, *Thalassia testudinum* (Kopecky and Dunton 2006). The adverse weather conditions typical of the tropical hurricane season generate current velocities sufficient for the removal of accumulated algal biomass (10 cm s^{-1}) (Biber 2007). Drift algae biomass varies by season as well as from 1 year to the next (Houk and Camacho 2010).

It has long been recognized that excessive quantities of drift macroalgae can have serious impacts on underlying seagrasses via competition for nutrients and PAR (Hauxwell et al. 2003). Excessive macroalgal loads can become so dense that they restrict water flow, thereby depriving seagrasses of oxygen and driving up concentrations of sulfides in the subsurface sediments (Holmer and Nielsen 2007). In addition to its impact on seagrasses, light attenuation by blooms of drift algae off the coast of Texas has caused significant reductions in seagrass epiphyte biomass (Kopecky and Dunton 2006). Given that the integrity of seagrasses can be severely compromised during these short-term seasonal blooms, the long-term repercussions of persistent blooms that may arise as a result of climate change demand serious consideration. Climate experts suspect that a changing climate will increase the number of intense storms and decrease those of intermediate intensity (Webster et al. 2005). The consequences of these changing weather patterns on the distribution of drift algae and their persistence within the coastal environment require close monitoring.

16.4.3.1 Calcareous Algae Within the Seagrass Habitat

High densities of seagrasses have the capacity to increase the pH of entire water bodies due to their uptake of CO_2 and release of OH^- (Beer et al. 2006). For example, *Cymodocea rotunda, Halophila ovalis,* and *Thalassia hemprichii* have the capacity to raise water pH from 8.1 to 8.6, 8.8, and 9.2, respectively (Beer et al. 2006). The pH compensation point of each species as well as the inability of seagrasses like *H. ovalis* to tolerate the high pH values and low inorganic carbon concentrations generated by the other two species forces these seagrasses into monospecific tide pools. However, Semesi et al. (2009) determined that calcifying macroalgae, such as *Hydrolithon* spp., *Mesophyllum* spp., and *Halimeda renschii*, can buffer against this increase in pH via intensified calcification. In fact calcification rates of *Hydrolithon* spp. can be five to six times higher in the presence of seagrasses. Similarly, photosynthetic activity of *Mesophyllum* spp. increased by 15% in the presence of seagrasses. Thus, when coexisting these two groups are capable of maintaining high levels of productivity while encouraging higher levels of biodiversity. Monitoring of the balance between these two groups is important as the dominance of one over the other could lead to dramatic shifts in water chemistry and a regime shift. Particularly important are the consequences that ocean acidification may have on this balance.

16.4.3.2 Regime Shifts and Controls Within the Seagrass Habitat

Human development of the coastal zone has often been identified as the source of nutrient pollution that disrupts the balance between seagrasses and macroalgae. In 2008, Houk and van Woesik collected evidence suggesting that seagrass species respond differently to environmental pressures. In a Saipan lagoon they found that increased watershed development stimulated macroalgal proliferation within *Halodule uninervis* seagrass meadows, severely impacting the integrity of the meadows. However, the same study revealed that the growth of a different seagrass, *Enhalus acoroides,* was positively correlated with human development and watershed size. The authors suggest that the physical and/or morphological characteristics of seagrass species determine their susceptibility to macroalgal overgrowth. Similarly, McGlathery (2001) suggests that *Thalassia testudinum* may be more resistant to the pressures of algal blooms because of a proportionately greater allocation of resources to below-ground biomass, allowing them to persist during temporary algal blooms.

The consequences of nutrient enrichment are not always easily predicted. Nutrient addition experiments in Florida resulted in increased seagrass biomass and decreased macroalgal epiphyte coverage offshore. Conversely, the inshore treatment had no effect on two species of seagrasses while macroalgae biomass increased significantly (Ferdie and Fourqurean 2004). In a similar Florida-based study, Armitage et al. (2005) found that enrichment of sediments stimulated highly variable group and site-specific responses by macroalgae. The resulting macroalgal blooms (calcareous green and filamentous red) were ephemeral and had no long-lasting impact on the system. Their results also showed that areas containing a high abundance of macroalgae were exposed to an array of additional chronic pressures including nutrient enrichment, current and erosion pressures, and heavy boat traffic. During nutrient treatments, phosphate (not nitrate) stimulated growth, prompting the researchers to conclude that Florida Bay is phosphate limited, a consequence of the high carbonate content of the sediments, perhaps owing to the calcareous algae contained therein. Results from a similar study in Puerto Rico show that several species of nutrient-depleted nuisance bloom (*Hypnea musciformis*) and mat-forming (*Acanthophora spicifera, Dictyota cervicornis*) macroalgae increased growth rates significantly when exposed to nutrient enrichment. However, enriched algae of the same species had no response to increased nutrient concentrations. Calcareous green algae (CGA) (e.g., *Halimeda incrassata*) did not respond to treatments within the 3-day experiment, suggesting limitation by some other metabolic process, such as calcification (Fong et al. 2003). Therefore, in order to predict the consequences of nutrient enrichment, coastal managers must consider the existing concentration of each relevant nutrient within the system as well as the primary producers contained therein.

Evidence suggests that storms arriving in the late summer cyclone/hurricane season play an important role in maintaining a balance between seagrasses and algae. Frequent disturbances such as large swells and intense currents prevent epiphyte growth and thus maintain seagrasses as the dominant flora (Houk and Camacho 2010). However, the impacts of massive natural disturbances on coastal systems (erosion, mechanical thinning, and burial) can completely transform benthic communities, often irreversibly. Following Hurricane Georges in 1998, Fourqurean and Rutten (2004) observed that while only 3% of *T. testudinum* was removed, 24% of CGAs were lost. CGAs are much more susceptible to hurricane damage because they lack the extensive rhizomes of seagrasses and are thus easily liberated from the substrate during sediment displacement. As the system recovered, CGAs were the first primary producers to recolonize bare patches, although its density did not return to prehurricane levels for another 3 years. This storm-dependent balance within the seagrass–algae complex and the biodiversity that it maintains can be considered within the context of the Intermediate Disturbance Hypothesis (Connell 1978).

16.4.4 Macroalgae–Mangrove Interactions

The vast majority of studies focused on mangroves come out of the Indian and Southwest Pacific Ocean in which water transparency can be low due to high tidal amplitude and intense terrestrial runoff typical of estuaries and deltas (Kristensen 2008). This limits subsurface primary productivity and promotes the development of detrital communities (Kristensen 2008). Studies coming out of Southeast Asia (Thailand, Malaysia) and the Indus Delta describe mangrove forests as nutrient exporting systems that have low epifaunal biodiversity, low macroalgal abundance, and organically rich sediments (Saifullah and Ahmed 2007). In this environment, macrophytes and filter feeding assemblages are extremely limited. As a result, many of the inhabitants are generalists and opportunists with microalgae and allochthonous phytoplankton providing an additional and essential source of nitrogen (Kristensen 2008). However, in the Atlantic Ocean and Caribbean Sea tidal amplitudes are minimal and terrestrial runoff is limited, leading to high water clarity, allowing for the proliferation of macroalgal and filter feeding communities within fringe regions (Kieckbusch et al. 2004). Therefore, the disproportionate amount of research coming out of Asia and Australia has led to a skewed perception of the role of macroalgae within mangrove systems.

16.4.4.1 Abundance and Productivity

The NPP (NPP) of mangrove prop root epiphytes in the Bahamas (8.5 ± 6.4 gC $\mathrm{kg^{-1}day^{-1}}$) has been measured to rival that of nearby seagrass epiphytes (Koch and Madden 2001). In the Karachi mangroves of the Indus Delta, Saifullah and Ahmed (2007) have estimated that the algal productivity is much higher than that of the mangroves themselves. However, the actual biomass of algae growing within some mangrove systems may be quite low due to light limitation. Nevertheless, their role in coastal food webs is likely to be consistently significant, owing to their nitrogen content, which is 10× higher than mangrove tissues (Alongi 1998). Since decomposition of mangrove tissues is a slow process, due to its high lignin, cellulose, and tannin content, it is likely that algae and bacteria provide a significant amount of nitrogen to the mangrove food web. Therefore, it is probable that any algal tissue appearing within algae-deficient mangrove habitats is likely to be quickly utilized by resident fauna (Alfaro 2008).

In 2001, Koch and Madden attempted to determine the source of nutrients within oligotrophic lagoons in the Bahamas. They found that total nitrogen and phosphorus concentrations were highest within fringe mangrove and seagrass meadow sediment samples directly adjacent to mangroves, relative to sand flats and open lagoon seagrass meadows. On a biomass basis, the gross primary production of prop root macroalgae was twice as high as nearby seagrass epiphytes and their NPP was even comparable to that of seagrasses. At that time they were unable to identify the cause of this nutrient gradient, but they suggested remineralization by bacteria, nutrient mobilization, and even delivery of metabolic wastes by fishes that migrate between habitats during the day.

Recently, a great deal of debate has been focused on whether or not mangrove systems are a source of nutrients for adjacent benthic and pelagic food webs (Kieckbusch et al. 2004; Bouillon et al. 2008). Of course, the retention of organic material within mangroves is completely dependent upon the tidal regimes of the area. For example, from their studies in Thailand, Kristensen (2008) suggests that the main source of organic matter in mangrove systems is derived from the mangroves themselves and that macroalgae contribute very little to the organic pool. Conversely, researchers in the Indus Delta argue that epiphytic algae are an important source of energy within the mangrove environment (Saifullah and Ahmed 2007). However, Bouillon et al. (2002) have provided evidence from studies in India, suggesting that there is very little export of this material to adjacent habitats. According to stable isotope analysis of benthic invertebrates in neighboring habitats, the labile organic matter that is exported from the mangroves is not consumed in significant quantities by faunal assemblages. Instead, grazers outside of the mangrove system prefer to consume local sources of algae which are likely to have a higher content of nitrogen. In fact, they argue that the primary production of mangrove epiphytes in Karachi is higher than that of mangrove trees. Therefore, caution must be taken when reviewing the literature and an understanding that each mangrove system is likely to be unique based upon hydrodynamics and algal communities.

16.4.5 Distribution of Macroalgae Within Mangroves

The mangrove systems of the Atlantic Ocean and Caribbean Sea are quite distinct from those of Asia and Australia, especially in the context of the importance of macroalgae. A recent study revealed that the most abundant epiphytes growing on mangrove prop roots in Panama were sponges and macroalgae (*Caulerpa verticillata* and *Halimeda* spp.) (Diaz and Rützler 2009). Sponges and macroalgae clearly compete for space on prop roots, with algae occasionally dominating where elevated sun exposure tips the balance in favor of algal dominance. In Belize, macroalgae only dominate where deforestation and dredging have recently occurred (Diaz and Rützler 2009). These two disturbances promote the suspension of fine sediments that negatively impact all filter feeders (sponges and ascidians), presenting the resulting macroalgal blooms with a competitive advantage.

Within mangrove habitats, algae growing on vertical surfaces are subject to an array of extremely variable conditions such as submersion and exposure, light, nutrients, temperature, and salinity. These challenging conditions have brought about the evolution of mangrove-specific algae. A survey of macroalgae growing on the pneumatophores of the mangroves of Karachi in the Indus Delta revealed a collection of 14 species belonging to Chlorophyta, Phaeophyta, and Xanthophyta phyla (Saifullah and Ahmed 2007). Within this habitat, algae and cyanobacteria covered 70–81% of the vertical length of mangrove pneumatophores. In Australia, species of macroalgae show a pattern of zonation along the vertical extent of the pneumatophores, likely arising as a result of competition, light exposure, and/or submersion/desiccation tolerance (Melville and Pulkownik 2007). Most algae are positioned above the low water mark where they are able to avoid extended periods of desiccation during the changing tides as well as maximize exposure to sunlight. Melville and Pulkownik (2007) suggest that species are arranged into three distinct ranges within the intertidal region according to their tolerance to desiccation. Low water mark algae are tolerant to submersion and have been suggested to be more aggressive competitors. High water mark algae are tolerant to desiccation and salinity changes (see Chap. 5 by Karsten) and the algae that are found in between these two groups are adaptable to both but have been so arranged as a consequence of competition.

16.4.6 Herbivory Within Mangroves

Studies have shown that many mangrove invertebrates rely on algae as a primary resource and some of them are likely to share symbiotic relationships with algae and/or their photosynthetic components (Bouillon et al. 2008). For example, an opisthobranch found in Indian mangroves feeds exclusively on red and green algae, sequestering the algal chloroplasts into its intercellular spaces in order to yield the products of continued photosynthesis (Bouillon et al. 2008). Grazers of the primary producers within the mangrove habitat (microphytobenthos, macroalgae, and mangroves themselves) are essential for channeling organic matter to higher trophic levels. Littorinids have been suggested as the dominant grazers of macroalgae growing on the vertical surfaces of mangrove prop roots, trunks, and branches and have even been said to have a “strong top-down force” in these coastal ecosystems (Alfaro 2008). Primary and secondary consumers, such as juvenile fishes and invertebrates, which inhabit the fringe of mangroves depend upon the roots of mangroves as a refuge alone and acquire most of their nutritional requirements from algal sources within the mangroves and seagrasses, as well as the seagrasses themselves (Kieckbusch et al. 2004). In 2004, Boyer et al. measured herbivory in three separate habitats dominated by seagrasses (*T. testudinum*), corals, and mangroves (*Rhizophora mangle*) off the northern coast of Honduras. Their results revealed that herbivores in all three habitats are capable of differentiating between food sources based upon nutritive value and thus preferentially grazed on nutrient-rich food items when given the opportunity. Compared to seagrass and coral habitats, overall macroalgae herbivory was lowest in the mangroves (31%, 33%, and 15%, respectively). However, the herbivores within the mangroves displayed the highest capacity for increased grazing (91%) following the nutrient enrichment.

Algae swept into the mangroves from adjacent rocky shore and estuarine habitats can become entangled in pneumatophores, persist, and at times reproduce to establish persistent free living colonies. It is suspected that these drift algae increase the likelihood of colonization by mollusks in mangroves by increasing substrate complexity and possibly serve as an additional food source (Bishop et al. 2009). The complex surface of fucalean macroalgae also represents an additional surface area for the growth of microfilms. Bishop et al. (2009) determined that algae originating from estuaries were capable of attracting more mollusks than algae coming from rocky shores. This is likely due to the typically higher nutrient content of estuarine systems which is capable of enriching algae and increasing its palatability for mollusks.

Some herbivorous fishes living within and adjacent to mangroves depend upon macroalgae growing as epiphytes on mangrove prop roots as a primary food source. For example, in Curaçao, the doctorfish, *Acanthurus chirurgus*, acquires approximately 55% of its macroalgal diet directly from mangrove surfaces (Nagelkerken and van der Velde 2004). The largest herbivorous reef fish in the Atlantic Ocean, *Scarus guacamaia*, is exclusively dependent on the mangrove habitat during its development and has suffered local extinctions where mangroves have been removed (Mumby et al. 2004). Of particular concern is the recent appearance of the invasive predatory lionfish, *Pterois volitans*, in Caribbean mangrove systems and the impacts that it will have on the recruitment of vital herbivorous fish species to adjacent coral reef habitats (Barbour et al. 2010; Albins and Hixon 2008).

16.5 Conclusion

Tropical macroalgae are essential elements of the complex coastal ecosystems they inhabit. They provide a wide range of vital ecological functions, like the stabilization of reefs, retention of nutrients, and provision of habitat and food. Macroalgae are able to provide all of these different functions due to their enormous diversity and habitat-specific adaptations. Over the last few decades, macroalgae have become more abundant across the globe, in coral reef, seagrass, and mangrove habitats, often as a response to human activities. At times, the proliferation of algae has led to regime shifts in these already threatened habitats. These ecosystem shifts have had profound consequences on tropical systems worldwide. In most cases a combination of coral mortality, eutrophication, reductions in grazing pressure due to disease, and overfishing form the basis for these shifts. In the near future, these shifts are likely to be exacerbated and prolonged, resulting in reduced overall habitat complexity and biodiversity.

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Chapter 17
Floating Seaweeds and Their Communities

Eva Rothäusler, Lars Gutow, and Martin Thiel

17.1 Introduction

Floating seaweeds have fascinated sailors and naturalists since the first ships sailed across the oceans, where they discovered immense rafts of seaweeds far from shore. Christopher Columbus was one of the first who documented dense aggregations of floating algae. In September 1492, his crew encountered masses of floating seaweed as they were approaching the Bahamas: "They saw so much weed that the sea appeared to be covered with it. . ..and there was a great deal of weed and they found crabs in it" (Farlow 1914).

Floating *Sargassum natans* and *S. fluitans* from the Sargasso Sea and especially their specifically adapted fauna are remarkable biological communities. Full-grown algae that form dense masses without ever having been attached to the seafloor pass their entire floating life cycle via the propagation of vegetative fragments (Parr 1939). While floating algal populations in other seas appear to originate from benthic source populations, the size of algal rafts and the length of their ocean voyages equal or even surpass that of *S. natans* and *S. fluitans*.

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Centuries after Columbus' voyage, contemporary marine scientists have reported floating seaweeds from all major oceans (Ohno 1984; Kingsford 1992; Helmuth et al. 1994; Ingólfsson 1998; Hobday 2000a; Hirata et al. 2001; Macaya et al. 2005; Vandendriessche et al. 2006; Komatsu et al. 2008; Hinojosa et al. 2010). Recent studies confirm that floating algae can cross large ocean basins, facilitating the colonization of new habitats on remote shores by the algae themselves but also by organisms living associated with floating algae (Fraser et al. 2009, 2011; Macaya and Zuccarello 2010; Nikula et al. 2010). Accordingly, these authors emphasized the importance of dispersal of organisms via these floating islands.

There is a wide variety of positively buoyant seaweeds in the oceans that become detached by breakage of stipes, thallus fragmentation, erosion of holdfasts, storms, or grazing activities. Once detached, floating seaweeds continue to grow if environmental conditions are optimal, and they form habitat for many associated organisms. Also these algae are known to travel considerable distances at the mercy of winds and currents, having the potential to release spores or gametes at a new site and thereby connecting distant populations (Fraser et al. 2009). In order to understand the fate of floating seaweeds it is crucial to address a set of questions. Where can we regularly find floating algae and where do they come from? How do abiotic and biotic factors affect the persistence of floating algae at the sea surface? How can floating algae acclimate or withstand sea surface conditions? Which organisms are traveling with them and how can they affect raft viability? Answering these questions will help to understand the role of floating algae as dispersal agents in the world's oceans.

17.2 Spatial and Seasonal Distribution of Floating Seaweeds

A wide diversity of seaweeds can be found floating in the world's oceans, where they persist at the sea surface thanks to the presence of gas-filled tissues or pneumatocysts (Fig. 17.1). The dominant floating seaweeds in the world's oceans are brown algae belonging to the genera *Macrocystis*, *Fucus*, *Sargassum*, *Ascophyllum, Durvillaea, Carpophyllum, Phyllospora,* and *Cystophora*. Some red and green algae have also been reported floating, albeit with a more limited floating potential than brown algae (Thiel and Gutow 2005a; Gagnon et al. 2011). Besides a few entirely pelagic species such as *Sargassum natans* and *S. fluitans*, most floating algae grow in benthic habitats during their earlier life stages and can vary widely in size after detachment, ranging from a few centimeters to tens of meters. Floating seaweeds can aggregate at the sea surface and form large rafts of many individuals with biomasses of up to 300 kg wet weight per seaweed patch (e.g., Senta 1962 for the Japanese coast) or more (Mitchell and Hunter 1970 for the southern Californian coast and Baja California).

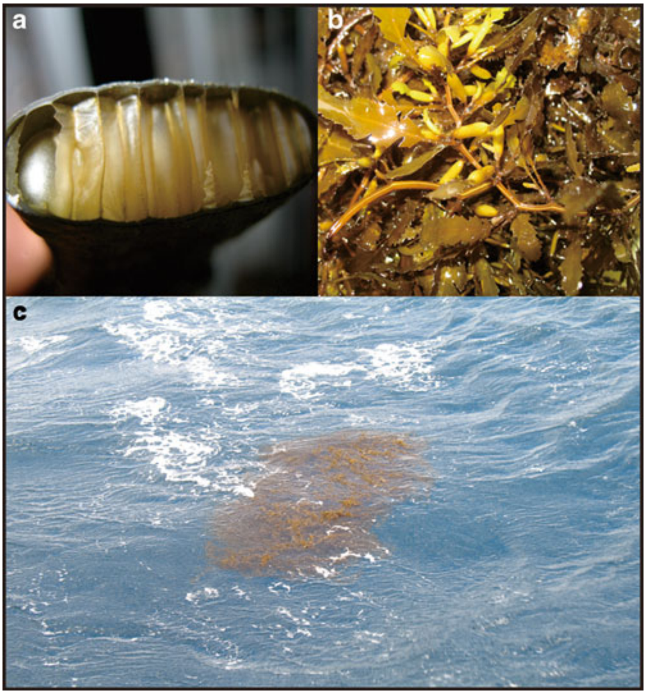

Fig. 17.1 (**a**) Cross section through a thallus of *Durvillaea antarctica* showing the gas-filled honeycomb structure; (**b**) vesicles of *Sargassum horneri*, providing positive buoyancy to the algae; and (**c**) raft of *S. horneri* floating in the eastern East China Sea

17.2.1 Global Distribution Patterns of Floating Seaweeds

The presence of floating algae at the sea surface strongly depends on their supply from benthic source populations. Most reports of floating macroalgae come from mid and high latitudes in both hemispheres (Kingsford 1992; Helmuth et al. 1994; Hobday 2000a; Macaya et al. 2005; Komatsu et al. 2008; Hinojosa et al. 2010; Thiel et al. 2011) (Fig. 17.2), where extensive benthic populations provide abundant supply (Lüning 1990; Graham et al. 2007). For instance, in the northern hemisphere algal rafts can be found in the NE Pacific where extensive subtidal kelp forests along the Pacific coast of North America nourish abundant floating populations of *Macrocystis pyrifera* (Kingsford 1995; Hobday 2000a). In the NW Pacific a diverse *Sargassum* community is floating in coastal waters around Japan (Ohno 1984; Hirata et al. 2001). In the N Atlantic pelagic *S. natans* and *S. fluitans* occur in the Gulf of Mexico, the Gulf Stream, and in the Sargasso Sea (Parr 1939) while floating fronds of *Ascophyllum nodosum* and *Fucus vesiculosus* are common along the northern N Atlantic >45°N (Tully and Ó Céidigh 1986; Ingólfsson 1998; Vandendriessche et al. 2006; Muhlin et al. 2008; Thiel et al. 2011).

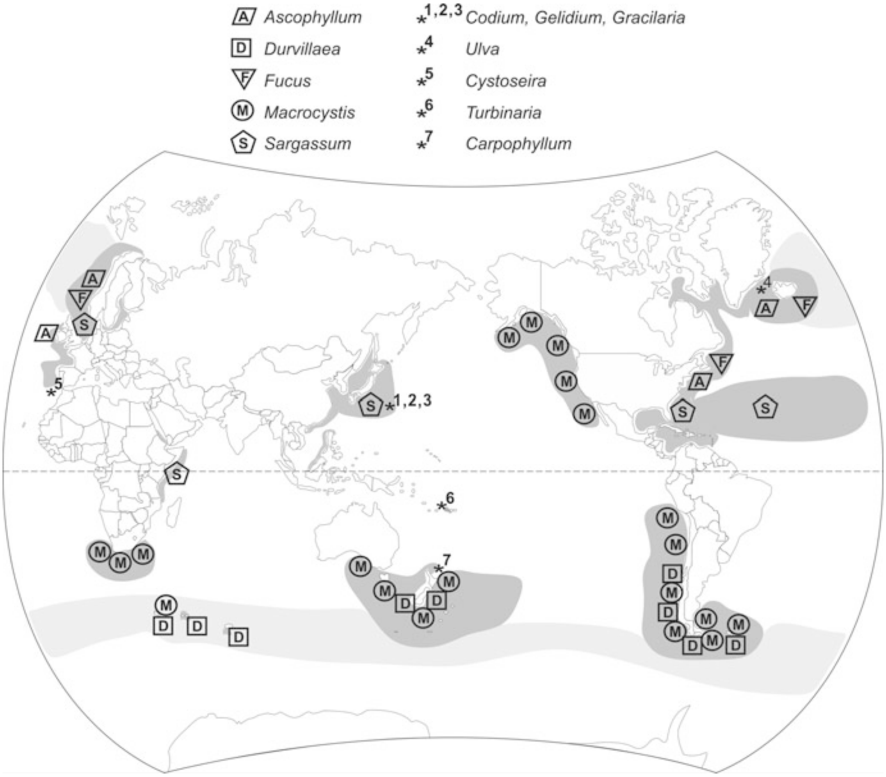

Fig. 17.2 Distribution of the most common genera of benthic algae (*indicated with symbols and letters*) that are positively buoyant, as well as examples of a few benthic genera (*indicated with asterisks and numbers*) that are less commonly found floating in the world's oceans. *Shadings* indicate areas where floating algae have been reported abundantly

M. pyrifera and *Durvillaea antarctica* are the most common floating seaweeds in the southern hemisphere. They occur in the SE Pacific along the Chilean coast (Macaya et al. 2005; Hinojosa et al. 2007, 2011), around Tasmania and New Zealand (Edgar 1987; Kingsford 1992) and throughout the entire West Wind Drift where floating sporophytes connect the algal populations of the sub-Antarctic islands (Smith 2002; Fraser et al. 2009). Also the Agulhas Bank region off South Africa "literally swarms with *Macrocystis*" (Hooker 1847). Whereas *Macrocystis* and *Durvillaea* are widespread throughout cold temperate waters of the southern hemisphere, other floating seaweeds have a more restricted distribution but may become locally very abundant. For example, high densities of floating *Carpophyllum* spp. and *Cystophora* spp. can be found in waters around New Zealand (Kingsford 1993) and buoyant *Turbinaria ornata* are common among the Polynesian islands (Stewart 2008). Although floating seaweeds can bridge large oceanic distances in subpolar regions, the warm waters of the tropics and the subtropics appear to be an impenetrable dispersal barrier mostly preventing the exchange of floating algae between the two hemispheres.

17.2.2 *Regional Aggregations of Floating Seaweeds*

Complex interactions between winds and mesoscale oceanographic features such as fronts, eddies, and currents determine the spatial distribution of algae at the sea surface. Accordingly, abundances of floating seaweeds vary substantially on a regional scale and are often highly unpredictable (Kingsford 1992; Ingólfsson 1998). For example, Kingsford and Choat (1986) observed consistently higher densities of floating algae inside than outside transient surface slicks, which were generated by tidally forced internal waves. In other regions, floating algae accumulate along fronts (Kingsford 1995) where single sporophytes may entangle at the sea surface to form large floating mats. Franke et al. (1999) reported that during calm summer conditions dense aggregations of floating algae form at boundary zones between tidal currents of different speeds and directions around the island of Helgoland (North Sea). Hinojosa et al. (2010) could show for the fjords of southern Chile that floating seaweeds are aggregated in an estuarine front in the large channel openings by an interaction of wind and the surface outflow of estuarine waters (Fig. 17.3). These regions are suggested to act as retention zones, which receive and accumulate floating seaweeds. Due to the aggregation of floating algae, other pelagic organisms, and organic matter, these retention areas are considered centers

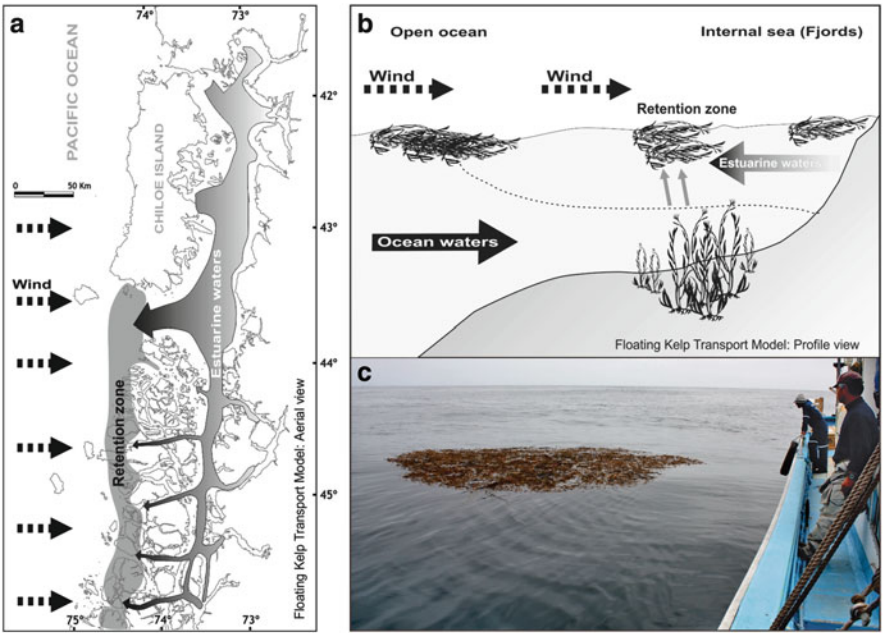

Fig. 17.3 Retention zones for floating seaweeds formed by winds, currents, and estuarine influence in the fjord regions of southern Chile, in (**a**) aerial view and (**b**) profile view; figure modified after Hinojosa et al. (2010). (**c**) Floating patch of *Macrocystis pyrifera*; image courtesy of Iván Hinojosa

of high biological activity, where decomposers that are associated with the floating algae recycle organic remains into nutrients and other compounds (Thiel and Gutow 2005b).

Floating seaweeds are often more abundant in coastal waters than in the open ocean (Segawa et al. 1961; Kingsford 1992; Ingólfsson 1995; Hobday 2000b). High nearshore densities of floating algae are primarily due to the proximity to coastal source populations. Additionally, floating algae are known to accumulate in coastal areas with complex current conditions and frontal zones (Segawa et al. 1961). Harrold and Lisin (1989) tracked floating *M. pyrifera* equipped with radio transmitters in coastal waters of California. They could show that the majority of algal rafts are deposited on beaches soon after detachment while others become entangled with benthic sporophytes in coastal kelp forests (see also Dayton et al. 1984; Graham et al. 1997). The onshore transport of floating *M. pyrifera* in coastal waters of California was confirmed by Hernández-Carmona et al. (2006) (Fig. 17.4). Results from experiments with artificial drifters revealed that directional net transport of floating algae in coastal systems is mainly the result of prevailing winds that interact with surface currents (Tapia et al. 2004). During periods of low wind, no substantial transport of the drifters by currents alone could be detected (Fig. 17.4). Apparently, only a relatively small fraction of detached seaweeds escapes to offshore waters where they might enter larger oceanic currents.

In offshore regions conspicuous amounts of seaweeds have repeatedly been observed in surface eddies that develop above seamounts in the NE Pacific (Parker and Tunnycliffe 1994). Additionally, floating algae often accumulate in the convergence zones of wind-induced Langmuir circulations (Faller and Woodcock 1964). In the N Atlantic, pelagic *Sargassum* has been observed in such windrows extending over tens to hundreds of miles (Carr 1986). Drift lines of floating *Sargassum* are transient structures that disintegrate when wind exceeds a certain threshold speed (Marmorino et al. 2011). Johnson and Richardson (1977) suggested that the downwelling of surface waters in the zones of convergence might carry *Sargassum* below a critical depth where the thalli lose buoyancy and finally sink to the seafloor, thereby exporting biomass from the surface to the deep sea benthos (Schoener and Rowe 1970).

17.2.3 Seasonal Patterns of Floating Populations

While large quantities of seaweeds appear during some periods of the year, floating algae can virtually disappear at other times. For instance, along the coast of Japan high densities of floating individuals of the annual *Sargassum horneri* can be found throughout spring and summer when the algae shed off most of their thalli during their reproductive season (Yoshida 1963; Ohno 1984; Hirata et al. 2001). Similar observations have been made by Kingsford (1992) for floating *S. sinclairii* from coastal waters of New Zealand, indicating that the appearance of large quantities of *Sargassum* is driven by their seasonal growth cycles. Additionally, the invasive

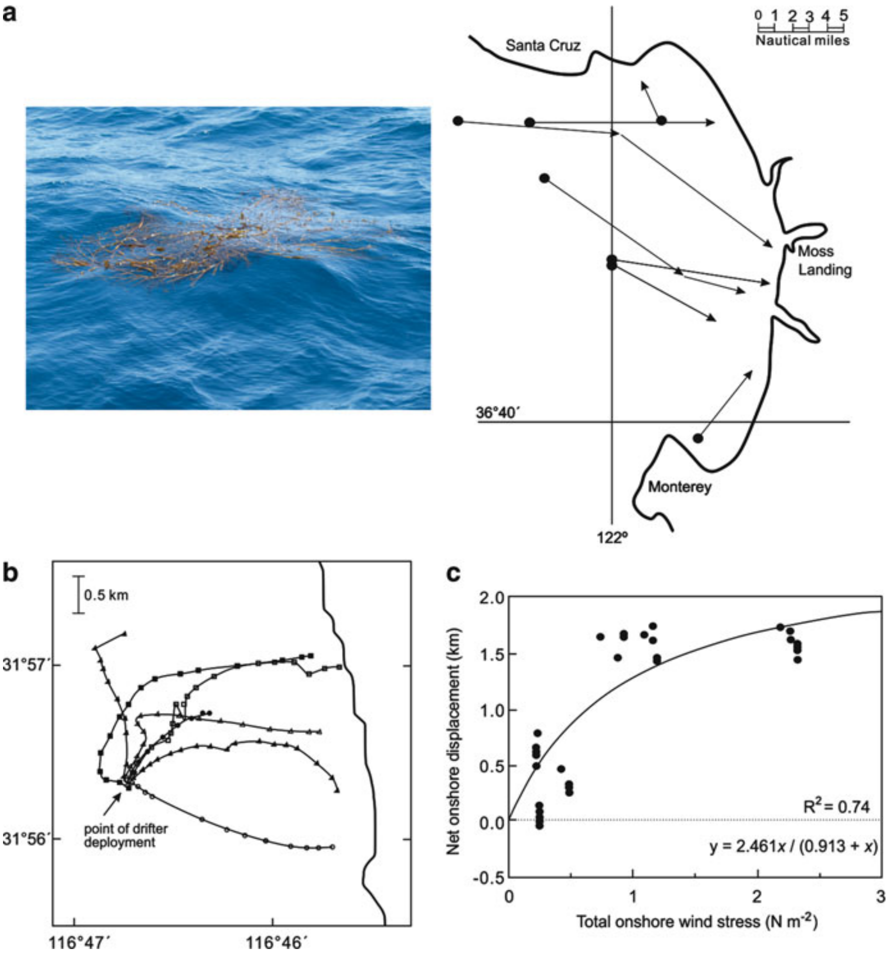

Fig. 17.4 Similar trajectories of (**a**) floating *Macrocystis pyrifera* and (**b**) artificial drifters towards the shore in coastal waters of California and Baja California, respectively. (**c**) Drift direction and velocity of the artificial drifters correlated with prevailing wind conditions. Figures modified after Hernández-Carmona et al. (2006) and Tapia et al. (2004)

species *S. muticum,* which originates from Japan, has been reported floating abundantly in May in the North Sea (Vandendriessche et al. 2006); thallus fragmentation and rafting dispersal may have facilitated the rapid spread of this species along the coasts of NW Europe (Rueness 1989; Harries et al. 2007). The holopelagic *Sargassum* species from the Gulf of Mexico seemed to have similar seasonal growth cycles, with highest amounts during March and June (Gower and King 2008). Seasonal variations of floating populations have also been revealed for perennial algae such as *M. pyrifera* and *D. antarctica* in southern Chile, with highest densities being found during austral spring (Hinojosa et al. 2010). Floating seaweeds can also reach high abundances after storms (Kingsford 1992), while during El Niño events, high water temperature and nutrient limitation can cause the disappearance of benthic seaweeds (Dayton et al. 1999), thus also leading to the elimination of the floating populations.

17.3 Ecophysiology of Floating Seaweeds

Growth and reproduction of floating seaweeds depend (as for their benthic counterparts) on a variety of abiotic and biotic conditions. At the sea surface, factors such as grazing activity, epibiont overgrowth, high water temperature, and solar radiation have been repeatedly inferred to have a negative effect on growth and health status of floating seaweeds. Also, it has been discussed that nutrient limitation might affect physiological functioning and growth of floating algae (Edgar 1987). While nutrient-limited open ocean waters suppress the physiological functioning of floating *S. natans* (Lapointe 1995), algae that accumulate in frontal systems where organic matter is efficiently recycled are thought to have sufficient nutrients to sustain algal growth (Thiel and Gutow 2005b).

Abrupt changes in environmental factors, as experienced especially by floating algae, can impact their photosynthetic apparatus, which is most susceptible to damage under stressful conditions. Stressed algae invest energy to adjust and maintain photosynthetic activity. However, this energy investment comes at the expense of algal growth. Consequently, algae respond with variable growth to changing environmental conditions because growth integrates all physiological costs and gains. Growth can be directly related to the overall health status of the algae and thus to their persistence at the sea surface (Fig. 17.5).

17.3.1 Light

At the sea surface floating algae are often exposed to intense visible (400–700 nm) and ultraviolet radiation (280–400 nm), which may induce photoprotective processes. In large outdoor mesocosm studies conducted along the Chilean coast, *M. pyrifera* reacted to high solar irradiance by lowering their pigment contents and by energy dissipation via heat (Rothäusler et al. 2011a, b). Similar physiological responses were observed for the holopelagic *S. natans,* floating in tropical waters of the Gulf of Mexico (Schofield et al. 1998). These processes are relevant because they permit algae to tolerate the stressful conditions of extreme irradiance and even to continue growing at the sea surface.

While the positively buoyant *M. pyrifera*, of which the attached sporophytes grow throughout the entire water column (up to 40 m in length), can efficiently acclimate to a broad range of irradiance prevailing along the Chilean Pacific coast (Rothäusler et al. 2011a, b), negatively buoyant seaweeds showed strong

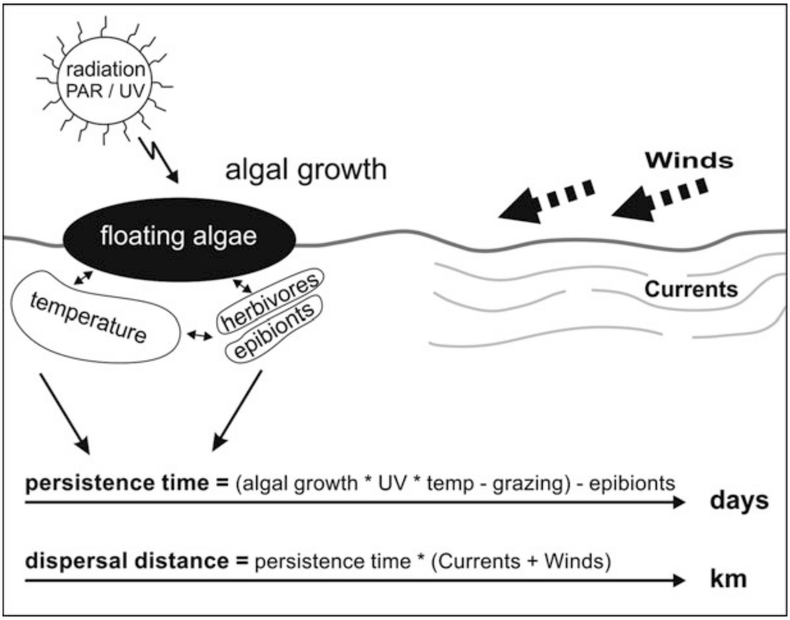

Fig. 17.5 Conceptual figure of the main abiotic and biotic factors affecting the growth of floating algae and thus their persistence at the sea surface

photoinhibition when transplanted close to the sea surface (Karsten et al. 2001). At low latitudes these photoacclimation responses were costly for *M. pyrifera*, which was reflected in their overall diminished growth responses, implying lower persistence due to combined effects of high water temperatures and high light conditions (Rothäusler et al. 2011a). While short-term exposure to UVA and UVB radiation induces the production of UV-absorbing phlorotannins in blades of benthic *M. pyrifera* (Swanson and Druehl 2002), at present it is not known whether floating *M. pyrifera* can also increase the phlorotannin content in response to elevated UV exposure as a protection of their photosynthetic tissues.

17.3.2 Temperature

Temperature is one of the most important factors controlling growth and persistence of floating seaweeds (Hobday 2000a; Rothäusler et al. 2009). For instance, algae from temperate waters lose biomass (Fig. 17.6), and thus floating capacity, when experiencing thermal stress on their floating voyages into warmer oceanic regions. Hobday (2000a) showed for the temperate *M. pyrifera* from southern California that the aging rate of kelp blades was low at surrounding water temperatures <20°C but substantially increased above this threshold. Recent

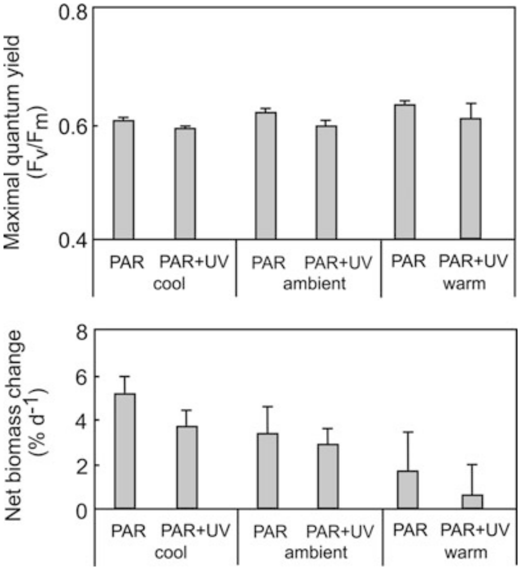

Fig. 17.6 Photosynthetic performance and growth of floating *Macrocystis pyrifera* maintained under different temperature and light conditions in outdoor mesocosm experiments. Figure modified after Rothäusler et al. (2011c)

studies in outdoor mesocosms confirmed that floating individuals of *M. pyrifera* lost biomass at water temperatures >20°C. A rapid disintegration of the algal thalli was observed at 24°C, where all algae sank after 5 days, even in treatments without grazers (Rothäusler et al. 2009). Similarly, floating persistence of temperate *A. nodosum* and *F. vesiculosus* from the southwestern North Sea was reduced at water temperatures >15°C due to high losses of biomass (Vandendriessche et al. 2007a). At equatorial latitudes in the Atlantic, John (1974) documented floating individuals of *A. nodosum* that were small (<0.5 m long) and not particularly robust. Possibly, high water temperatures are responsible for the rapid demise of floating algae in these oceanic regions. Besides temperature, also desiccation may affect the physiological functioning and thus the disintegration of algae, but this effect probably depends on the degree of buoyancy of each algal species (Thiel et al. unpublished).

Suboptimal water temperatures can also affect the reproductive activity of floating algae (Macaya et al. 2005; Rothäusler et al. 2009) (Fig. 17.7). Along the Chilean Pacific coast, in situ sampling and mesocosm experiments with floating *M. pyrifera* confirmed the absence of reproductive tissues (sporophylls) at low latitudes, while at higher latitudes many rafts had fertile sporophylls (Macaya et al. 2005). The authors inferred that unfavorable sea surface conditions, such as water temperatures >20°C, at low latitudes are responsible for the observed pattern. Overall, results imply that low water temperatures (and possibly also winter conditions) favor the persistence and reproductive success of temperate species at the sea surface, which consequently have higher potential for long-distance dispersal.

Contrary to meropelagic rafts, the tropical holopelagic *S. natans* and *S. fluitans* in the Sargasso Sea have growth optima and thus an optimal persistence at

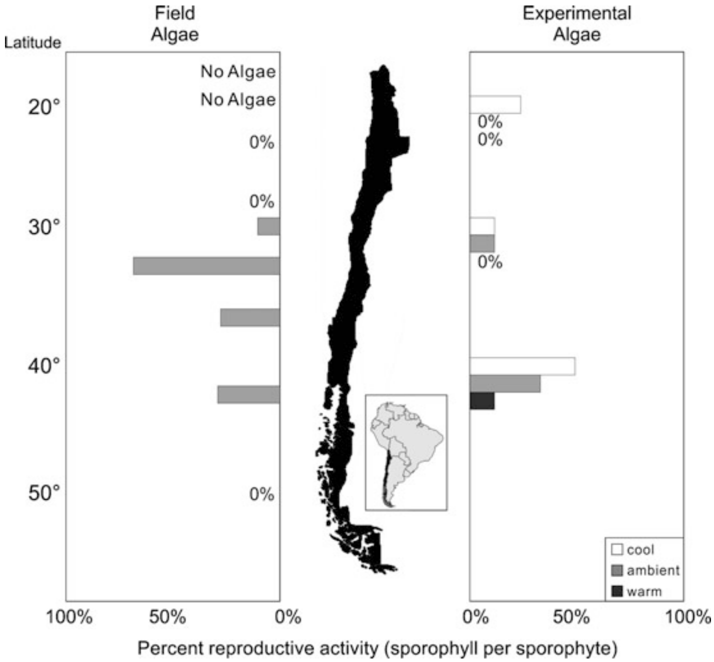

Fig. 17.7 Percent reproductively active sporophytes of freely floating *M. pyrifera* and in outdoor mesocosm experiments simulating the temperature gradient (ambient, cool, warm) along the Chilean Pacific coast. Figures modified after Macaya et al. (2005) and Rothäusler et al. (2009), respectively

temperatures between 18°C and 30°C (Hanisak and Samuel 1987). These algae, commonly known as gulfweed, appear to have evolved efficient protection mechanisms to endure surface levels of high temperature and irradiance (Schofield et al. 1998 for *S. natans*), which is in accordance with their distributional ranges in the tropical and subtropical N Atlantic. No growth was revealed for both species at water temperatures around 12°C (Hanisak and Samuel 1987).

17.3.3 Herbivory

Floating seaweeds are commonly inhabited by dense populations of mobile mesoherbivores such as amphipods and isopods, which can affect algal persistence by removing photosynthetic tissue and thereby weakening the ability to fix carbon (Gutow 2003; Thiel and Gutow 2005b; Vandendriessche et al. 2007a; Rothäusler et al. 2009). These grazers mainly feed on vegetative blades and it was shown for floating individuals of *M. pyrifera* in an outdoor mesocosm study that high densities of a herbivorous amphipod led to a reduction in pigment contents (e.g., by the

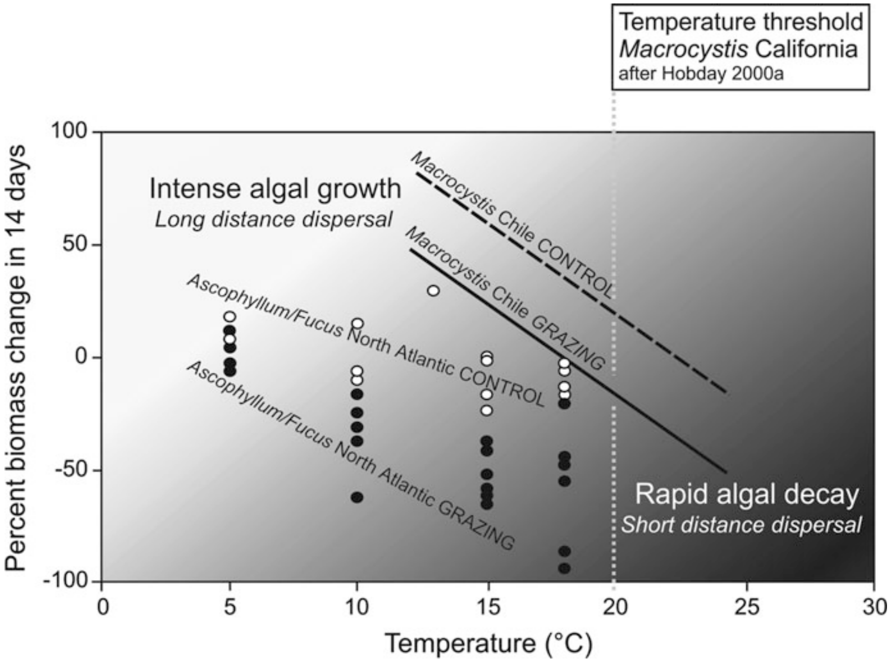

Fig. 17.8 Conceptual model of the influence of the combined effects of temperature and grazing (CONTROL versus GRAZING) on percent biomass change of floating algae during 14 days; data for *Ascophyllum nodosum* and *Fucus vesiculosus* were taken from Vandendriessche et al. (2007a), and data for *Macrocystis pyrifera* from Rothäusler et al. (2009)

allocation of N to the synthesis of other compounds) and algal growth at mid latitudes (Rothäusler et al. 2009, 2011b), while under moderate grazing pressure algae could compensate tissue loss by enhanced growth (Cerda et al. 2009). Grazing by isopods also provoked fast sinking of *A. nodosum* and *F. vesiculosus* but it seemed that the destructive effects of the grazers depended on water temperature and the availability of alternative food resources (Gutow 2003; Vandendriessche et al. 2007a). The negative effect of isopod grazing on the floating potential of the algae was enhanced by high water temperatures, which resulted in a reduced persistence of the brown algae at the sea surface (Vandendriessche et al. 2007a). Contrarily, in cooler waters (<15°C) grazing seemed to play only a minor role for the survival of floating algae because they can compensate grazer-induced tissue losses via growth (Vandendriessche et al. 2007a; Rothäusler et al. 2009) (Fig. 17.8). This might also explain why Ingólfsson (1998) observed no signs of decay in *A. nodosum* after >40 days of floating in cold Icelandic waters.

17.3.4 Epibiosis

Floating seaweeds are commonly colonized by larvae of sessile epibionts such as bryozoans and lepadid barnacles (Thiel and Gutow 2005b), which can influence algal growth by covering photosynthetic tissues. At mid latitudes in the Humboldt Current System, it was observed that bryozoan cover of *M. pyrifera* increased with distance from potential source populations and that physiological parameters (e.g., maximal quantum yield and overall photosynthetic efficiency) declined with increasing bryozoan size (Rothäusler et al. 2011d). Small benthic algae can maintain high photosynthetic activity under bryozoan cover by increasing the pigment content (Muñoz et al. 1998). However, such shade adaptation was not observed in benthic and floating *M. pyrifera* (Hurd et al. 2000; Hepburn et al. 2006; Rothäusler et al. 2011d). While dense epibiont cover can increase the specific density of floating algae and even cause sinking, uncalcified young bryozoan colonies might have a positive effect on algal tissue by shielding them against high solar radiation. Algae may also benefit from encrusting bryozoans through the provision of carbon dioxide and ammonium released directly from epibionts onto the algal tissue (Muñoz et al. 1998; Hurd et al. 1994, 2000), but these advantageous effects probably depend on the degree of colonization. In general, over long floating times, continuous epibiont growth and grazing pressure negatively affect algal persistence at the sea surface. However, depending on the presence of alternative food sources and the colonization progress, not all organisms associated with floating algae (e.g., detritus feeders, scavengers, and predators) may have the same destructive effects on their rafts.

17.4 Rafting Communities

Floating seaweeds carry with them a wide diversity of organisms (Thiel and Gutow 2005b and references therein). The composition of the rafting community and the abundance of individual species can be highly variable in time and space, and successional changes are probably related to travel time of the floating algae, their distance from the shore, competition, and predation.

Not all organisms are equally adapted to the rafting life style because not all of them can efficiently hold onto floating algae. Large invertebrates such as sea urchins, crustaceans, and gastropods immediately drop off when detached algae float to the sea surface. Also small organisms such as the boring peracarid isopods *Limnoria* spp. quickly left their burrows after kelp holdfasts were detached from benthic substrata (Miranda and Thiel 2008). Similarly, Gutow et al. (2009) showed that the densities of some peracarid crustaceans dropped immediately after algae became dislodged. Some species, such as ampithoid amphipods that build nest-like domiciles on algal blades (e.g., *Peramphithoe femorata* Cerda et al. 2010), may persist and even reproduce after detachment, resulting in a population increase during rafting journeys (see also Thiel 2003). Even though these motile organisms can stay and proliferate on algal rafts, other effective rafters are sessile organisms such as hydrozoans and bryozoans, which can form dense colonies on algal blades where they overgrow each other when competing for space (Thiel and Gutow 2005b and references therein). Some of these sessile epibionts colonize the rafting substrata at a later stage via the propagules from the water column.

The most common marine invertebrates on floating algae are peracarid crustaceans, which incubate their embryos in a marsupium, from which fully developed juveniles emerge. Direct development has been considered an important life history trait for rafters, because offspring can immediately recruit onto the algae (Ingólfsson 1998; Gutow 2003; Thiel and Haye 2006; Vandendriessche et al. 2006). Thus, their populations might not only persist but also increase over time. This mode of local recruitment is advantageous for rafters, since local populations on the algae can be maintained, even when the duration of the rafting journey exceeds the lifetime of the species (Thiel and Gutow 2005b). Direct development also favors successful colonization of new habitats.

17.4.1 Successional Changes of Epibiont Communities on Algal Rafts

Rafting communities can experience substantial changes during their journey. These changes are immediately initiated with the detachment of the algae from the benthic substratum (Kingsford and Choat 1985; Miranda and Thiel 2008; Gutow et al. 2009) and continue throughout the entire floating period. For instance, Helmuth et al. (1994) reported that with distance from their benthic source populations, kelp rafts had more sessile epibionts. Vásquez (1993), who tethered kelp holdfasts to a main line, demonstrated that densities of associated peracarid crustaceans increased towards the end of the experiment. In natural algal rafts around Iceland, Ingólfsson (1995) observed that the diversity of associated organisms decreased with increasing distance from source regions.

These temporal changes of rafting communities can be influenced by species interactions. Floating seaweeds attract fish (Kingsford 1992, 1995) and seabirds (Vandendriessche et al. 2007b), which prey upon associated organisms, thereby suppressing the populations of these organisms (including small grazers) on the rafts. In addition, rafters may compete with each other for food and space, which also affects species succession during a long voyage (Tsikhon-Lukanina et al. 2001).

17.5 Rafting Dispersal of Seaweeds and Associated Organisms

The dispersal of algae and their associated organisms strongly depends on the persistence of the rafts at the sea surface and on the capability of the organisms to withstand the rafting conditions. Under favorable conditions, algae can continuously grow and thus provide a long-lasting food source for herbivorous passengers. The floating thalli of, e.g., *M. pyrifera* even continue to reproduce while afloat, thereby acting as successful spore carriers, dispersing over hundreds of kilometers (Macaya et al. 2005; Hernández-Carmona et al. 2006). Thus, floating rafts facilitate population connectivity and expansion of geographic ranges of the floating algae themselves and of associated organisms. Winds and ocean currents mainly determine the floating directions, velocities, and distances that algae can cover.

17.5.1 Floating Velocities and Trajectories

Driven by the major oceanic currents, floating algae are transported across the world's oceans. While ocean currents determine large-scale algal movements, strong winds largely influence algal dispersal on a regional scale. Overall both forces in combination determine algal trajectories and velocities (Thiel and Gutow 2005a and references therein).

Following patches of *M. pyrifera*, Harrold and Lisin (1989) showed that rafts within Monterey Bay (California) occasionally move very slowly and at other times can advance very fast (0.2–2.3 km h^{-1}). Within the southern California Bight a similar trend was observed by Hobday (2000b) for satellite-tracked drifters. Very high velocities of up to 0.8 km h^{-1} have also been reported for algae floating in southern Japan (Segawa et al. 1962; Yoshida 1963), which are probably related to the prevailing current velocities (Thiel and Gutow 2005a).

Trajectories of floating algae and their associated organisms closely follow the directions of the major current systems (Thiel and Gutow 2005a). For instance, Helmuth et al. (1994), who sampled *M. pyrifera* rafts, underlined the importance of the West Wind Drift in the Southern Ocean in transporting algae in eastward direction between South America and sub-Antarctic islands (see also Chap. 14 by Huovinen and Gómez). A similar route in the West Wind Drift had been reported for *D. antarctica* (Smith 2002). Along the Chilean Pacific coast, within the Humboldt Current, floating seaweeds are generally displaced towards the north (Macaya et al. 2005) but southward movements are also observed occasionally. In the N Pacific, Hobday (2000b) underlined that floating *M. pyrifera* are transported in southward direction within the Californian Current. These observations confirm that algal rafts together with their passengers are transported with the main oceanic currents, both across vast areas of open ocean and over extensive distances in alongshore direction.

17.5.2 Connectivity of Populations

There is increasing evidence from molecular studies confirming population connectivity of floating seaweeds and their associated fauna (e.g., Thiel and Haye 2006 and references therein; Muhlin et al. 2008; Fraser et al. 2009; Coleman and Kelaher 2009; Nikula et al. 2010; Coyer et al. 2011; Buchanan and Zuccarello 2012). Bull kelp *D. antarctica* showed high genetic homogeneity among populations from different sub-Antarctic islands (Fraser et al. 2009) (Fig. 17.9). Similarly, results by Macaya and Zuccarello (2010) showed that a single haplotype of *M. pyrifera* dominated the populations from sub-Antarctic islands that are separated by thousands of kilometers (see green dots in Fig. 17.9). Results of both studies show strong evidence that *D. antarctica* and *M. pyrifera* can occasionally be transported across some of the world's largest gaps of open ocean (Fig. 17.9). Efficient dispersal of these floating kelps and of associated organisms is facilitated by the West Wind Drift, the strong surface current moving steadily in eastward direction (Waters 2008). Rafting on seaweeds can thus transport epifaunal organisms to distant shores as confirmed by, e.g., Nikula et al. (2010) for two peracarid crustaceans inhabiting the holdfasts of *D. antarctica*.

Algal rafting also contributes strongly to population connectivity over smaller spatial scales. The fucoid alga *Phyllospora comosa* from eastern Australia showed gene flow between populations that were separated by a 70-km distributional gap (Coleman and Kelaher 2009). Similarly, Muhlin et al. (2008) confirmed connectivity between *Fucus vesiculosus* populations from two adjacent peninsulas in the Gulf of Maine. Results suggest that floating of fertile thalli, which can release gametes when reaching a new site, is responsible for population connectivity. Floating dispersal also seems to affect the genetic population structure of some species of *Sargassum* along the coasts of SE Asia (Cheang et al. 2010, but see also Uwai et al. 2009). Along the European Atlantic coast, there is evidence of high genetic homogeneity between populations of *A. nodosum* (Olsen et al. 2010) and similar

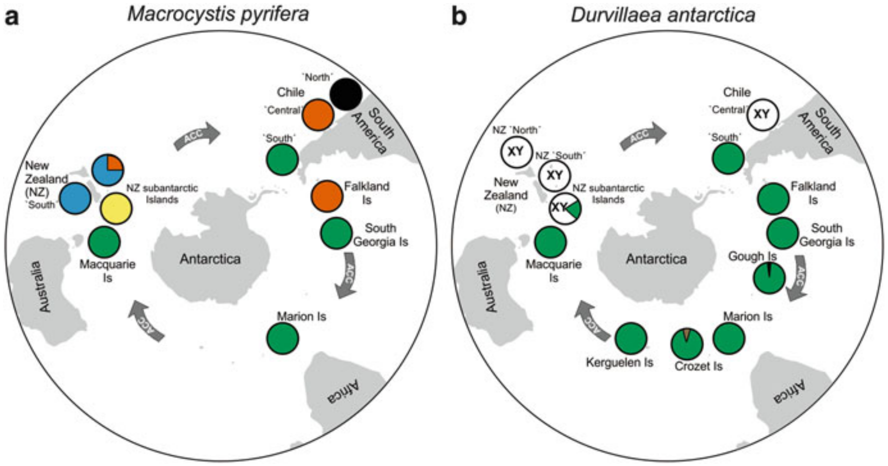

Fig. 17.9 Map of the sub-Antarctic region with different haplotype distributions for (**a**) *Macrocystis pyrifera* and (**b**) *Durvillaea antarctica*. *Different colors* indicate distinct haplotypes and XY denotes other haplotypes as shown. ACC: Antarctic Circumpolar Current. Figures modified after Macaya and Zuccarello (2010) and Fraser et al. (2009, 2010), respectively

results were shown for *Cystoseira amentacea* var. *stricta* from the Mediterranean Sea (Susini et al. 2007). While *A. nodosum* is highly buoyant, individuals of *C. amentacea* var. *stricta* lack vesicles but thallus fragments mix with other floating algae at the sea surface (Susini et al. 2007). Overall, the dispersal of gametes and spores via floating reproductive fragments or adults may also facilitate the reestablishment of algal populations after large-scale disturbances (such as El Niño events) (e.g., Dayton et al. 1999).

17.6 Outlook

Floating seaweeds can be found from the tropics to the Arctic and the sub-Antarctic islands. Since most studies on the physiology and ecology of floating algae were conducted at mid and high latitudes (e.g., Hobday 2000a, b; Macaya et al. 2005; Rothäusler et al. 2009), our knowledge about floating algae from tropical and subtropical regions is scarce. We propose that future research should examine the floating persistence of algae traveling in warm waters and under high radiation conditions, which will help to understand the role of low latitude algae as potential dispersal agents. In the face of global climate change, which predicts to drive species ranges towards the poles (see also Chap. 18 by Bartsch et al.; Parmesan and Yohe 2003), it can be expected that tropical and subtropical algae with positive buoyancy might expand farther towards mid latitudes, while the dispersal potential of temperate floating algae will be suppressed at mid latitudes (see above).

While afloat, algae can be concentrated in frontal systems (convergence zones) and eddies, which can result in the formation of huge biomass accumulations (e.g., Gower et al. 2006). Particulate organic matter such as algal detritus can also aggregate within these zones, contributing to biogeochemical cycles (Thiel and Gutow 2005b). Decomposers may use the organic matter as a substrate and nutrients released can be assimilated by the algae. Efforts should be made to better understand these processes within zones where floating algae and other floating items accumulate (Hinojosa et al. 2011).

So far, molecular studies have helped to reveal population connectivity of seaweeds and associated organisms over a broad range of spatial scales. However, they should also include the temporal scale. Rafting frequencies mainly depend on the availability and the persistence of the floating algae at the sea surface. Depending on latitude and local conditions, supply of floating algae can be spatially and temporally variable. Furthermore, the benthic distribution of floating algae might have changed substantially over evolutionary and ecological timescales. Future studies should therefore not only examine the relevance of rafting for recent population connectivity, but also how episodic rafting in the past has facilitated the establishment of isolated populations and subsequently led to allopatric speciation.

17.7 Conclusions

Floating seaweeds are an important component of the pelagic environment, predominantly in cold temperate and subpolar regions. Although most of the common floating algae naturally grow in benthic environments, these species show specific adaptations to the floating lifestyle which allow for persistence at the sea surface over prolonged time periods. These adaptations indicate selection for traits that facilitate floating persistence, suggesting that floating is a common and integral part of the species' life cycle (see e.g., Rothäusler et al. 2011a). Long-term floating supports genetic exchange between distant populations, natural range expansion, and regional population persistence through re-colonization after local extinctions.

Floating seaweeds significantly contribute to the complexity of the pelagic environment providing habitat for a rich community of associated rafters. Large patches of floating algae can be considered biodiversity hotspots, which catalyze the accumulation of species and the development of interspecific interactions among rafters and with their algal raft. For the associated rafters the patches of floating algae provide a highly dynamic habitat, which is subject to continuous changes depending on fluctuations of the biotic and abiotic environment. Considerable changes of the algal habitat during the pelagic journey are likely to exert strong selective pressure on the associated rafters.

Genetic homogeneity among distant populations of seaweeds and associated rafters, especially in the southern ocean, is the result of continuous exchange of floating individuals across extensive areas of open ocean. Continuous large-scale dispersal via floating algae adds a cosmopolitan dimension to marine biogeography that might not have been achieved through dispersal of larvae and spores alone.

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Part IV

Effects of Global and Local Changes on the Performance of Seaweeds

Chapter 18
Global Seaweed Biogeography Under a Changing Climate: The Prospected Effects of Temperature

Inka Bartsch, Christian Wiencke, and Thomas Laepple

18.1 Introduction

Climate changes and concurrent changes in temperatures, atmospheric CO_2 concentration, and other greenhouse gases have often occurred during the earth's history (Zachos et al. 2008) and it is well known that biogeographical distribution patterns of species are directly controlled by climate (Pearson and Dawson 2003 and references therein). Considering only the last 740,000 years, we know of about eight glaciations associated with strong variations in temperature, precipitation, and thermohaline circulation worldwide (Augustin et al. 2004; Knutti et al. 2004). In the past century, overall global warming was around 0.8°C (Hansen et al. 2006). Changes are particularly strong in polar and cold-temperate regions of the northern hemisphere (Levitus et al. 2000; Hansen et al. 2006). At the western Antarctic Peninsula a recent rapid regional warming with a sea surface temperature (SST) increase of 3.7°C century^{-1} has been recorded (Vaughan et al. 2003). Massive retreat of icefronts and glaciers and an increase of melt water production has been documented since 1956 (Braun and Gossmann 2002). For the Arctic, a similar warming trend has been observed over recent decades. Monthly temperature anomalies can be as large as 3–4°C (Turner et al. 2007). In cold- and warm-temperate localities, the reported mean annual temperature increase was as high

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as >2°C depending on location and duration of time series within the last decades (e.g., California: Sagarin et al. 1999, Portugal: Lima et al. 2007, North Sea: Wiltshire et al. 2008, Baltic: Andersen et al. 2011, Australia: Poloczanska et al. 2011). Current warming is larger over landmasses than over the open ocean and is larger in higher latitudes than in the tropical region. In the Equatorial Tropical Atlantic and the Western Equatorial Pacific (WEP), the SST increase between 2001 and 2005 relative to 1870–1900 was 0.5–1°C, while the Eastern Equatorial Pacific (EEP) did not show any temperature increase (Hansen et al. 2006). Whether the increased temperature difference between the near-equatorial WEP and EEP may be responsible for dampening or enhancing the frequency of El Niño-Southern Oscillation (ENSO) activity is still in debate (e.g., Hansen et al. 2006; Collins et al. 2010). The two most pronounced ENSO events in the last 100 years took place in 1983 and 1998 accompanied by an unprecedented warming in the EEP (Hansen et al. 2006).

Within the last two decades, there have been many attempts to develop predictive modeling approaches to project present-day biogeographical distribution patterns into the future. Principally, two different directions have been followed: (1) the "bioclimate envelope" models correlate species distributions with climate variables including the knowledge about the physiological responses of species to climate change (Pearson and Dawson 2003 and references therein). A special form of these models is niche modeling which correlates the macroecological preferences of a species at sample locations (e.g., demands for temperature, substrate, light, etc.) with their distributional records. Niche models predict potentially suitable habitats and the fundamental biogeographical niche (Guisan and Thuiller 2005; Graham et al. 2007; Verbruggen et al. 2009). (2) On the other hand, marine ecologists stressed the importance to also consider the variety of biotic interactions between species which are mostly responsible for shaping the realized niche. A recent review extensively summarizes possible consequences of both the abiotic and biotic environment and their interactions in coastal marine environments with respect to climate change (Harley et al. 2006). Although biotic interactions locally shape communities, they do not explain global biogeographical patterns (Santelices et al. 2009). Recently, Müller et al. (2009, 2011) presented a new bioclimate envelope model comparing observed winter and summer SSTs of 1980–1999 to model SSTs of 2080–2099 based on a moderate greenhouse gas emission scenario in order to predict future distributional range shifts of selected polar and cold-temperate seaweed species of both hemispheres. Here, we use the same approach providing a macroecological view on seaweed distribution based on a worldwide model of present and future oceanic isotherms, carving out the resulting changes in spatial extent of major biogeographical coastal regions (after Briggs 1995) due to temperature change and discussing expected changes of seaweed floras on a worldwide scale for the end of the century.

18.2 Coastal Marine Biogeographical Regions and Their Relation to Oceanic Isotherms and Temperature Responses of Seaweeds

Especially temperature changes had and will have strong effects in the geographical distribution of seaweeds as temperature is the main abiotic factor directly controlling geographic boundaries of seaweed species (van den Hoek 1982a; Lüning 1990; Chap. 3 by Eggert) and also has recently been identified in shaping global marine biodiversity pattern (Tittensor et al. 2010). Principally, the presence of seaweeds in these regions is determined by the physiological tolerance of their life cycle stages to temperature. There are two fundamentally different types of temperature boundaries in seaweeds, lethal boundaries and growth or reproduction boundaries (Breeman 1988; van den Hoek and Breeman 1989). Lethal boundaries are determined by the capacity of the species to survive during the unfavorable season, e.g., a cold-water alga in the summer season. Growth and/or reproduction boundaries are determined by the ability of the species to grow and reproduce during the favorable season, e.g., a cold-water alga in the winter/spring season. Moreover, seaweed distribution is affected by temperature–daylength interactions (Dring 1984; Molenaar 1996) affecting the coordinated timing between life cycle stages.

Seven broad biogeographical regions have been recognized in coastal marine zoogeography and phytogeography (Briggs 1974, 1995; Lüning 1990): the tropical region of the Atlantic and Indo-Pacific, the cold- and warm-temperate regions of both hemispheres, and the two Polar regions (for details see Chap. 3 by Eggert). Although Spalding et al. (2007) recently proposed a new and more sophisticated global system of marine ecoregions than Briggs (1995), the major biogeographical boundaries along the continents are similar in both approaches. We therefore chose the Briggs (1995) system as it is better suited for demonstrating the broad global pattern of modeled future change. The boundaries between biogeographical regions after Briggs (1995) are determined by fundamental changes in the composition of coastal biota and have been defined by their degree of endemism (>10%; Spalding et al. 2007). The transition between regions may be characterized by SSTs as temperature is a major factor in shaping marine phytogeographical regions (e.g., van den Hoek 1982a, b; Lüning 1990). Lüning (1990) described the boundaries of phytogeographical regions by intermediate mean summer and winter isotherms to show the general broad pattern. The specific mean summer and winter isotherms prevailing at the eastern and western coasts of the Oceans and in the northern and southern hemisphere at the phytogeographic boundaries deviate, however, considerably from these averages and are presented in Table 18.1 based on isotherm data from 1980 to 1999 provided by Müller et al. (2009).

The current tropical coastal biogeographical regions are broad and characterized by summer isotherms between 24 and 29°C and winter isotherms between 18 and 23°C (Table 18.1, Figs. 18.1a and 18.2a). The adjacent warm-temperate regions are much smaller and generally slightly compressed on the western sides of the Pacific

Table 18.1 Biogeographic regions after Briggs (1995) with the respective northern and southern mean oceanic sea surface isotherms limiting the respective region derived from global sea-surface isotherm maps 1980–1999 (Müller et al. 2009)

	Biogeographic region		Atlantic				Pacific				Indic			
			Western coastlines		Eastern coastlines		Western coastlines[a]		Eastern coastlines		Western coastlines[c]		Eastern coastlines	
			Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer
Northern hemisphere	Polar-Arctic	SB	<0°C	<10°C	<0/2°C[b]	<9°C	<0°C	<9°C	<0°C	<9°C	–	–	–	–
	Cold-temperate	NB	0°C	10°C	0/2°C[b]	9°C	0°C	9°C	0°C	9°C	–	–	–	–
		SB	10°C	27°C	10°C	17°C	12/14°C[c]	26°C	14°C	18°C	–	–	–	–
	Warm-temperate	NB	10°C	27°C	10°C	17°C	12/14°C[c]	26°C	14°C	18°C	–	–	–	–
		SB	23°C	29°C	21°C	27°C	22°C	29°C	20°C	26°C	–	–	–	–
	Tropical	NB	>23°C	>29°C	>21°C	>27°C	>22°C	>29°C	>20°C	>26°C	–	–	–	–
Southern hemisphere		SB	>22°C	>27°C	>18°C	>24°C	>21°C	>27°C	>21°C	>26°C	20°C	24°C	21°C	25°C
	Warm-temperate	NB	22°C	27°C	18°C	24°C	21°C	27°C	21°C	26°C	20°C	24°C	21°C	25°C
		SB	10°C	19°C	–	–	14°C	20°C	11°C	16°C	–	–	14°C	18°C
	Cold-temperate	NB	10°C	19°C	–	–	14°C	20°C	11°C	16°C	–	–	14°C	18°C
		SB	–	–	–	–	–	–	–	–	–	–	–	–
	Polar-Antarctic	NB	Winter: <1°C / Summer: <4°C											

SB southern boundary, NB northern boundary, – no exact data available as there are no further land masses south of the continents in the southern hemisphere or in the case of the Indian Ocean no ocean-land boundaries further north

[a] The border of the W-Pacific to the Indian Ocean was considered to be located in central Asia (northern hemisphere) and in southeastern Australia (southern hemisphere)

[b] Temperature boundaries for Barents Sea/North Atlantic

[c] Temperature boundaries for Korea/Japan

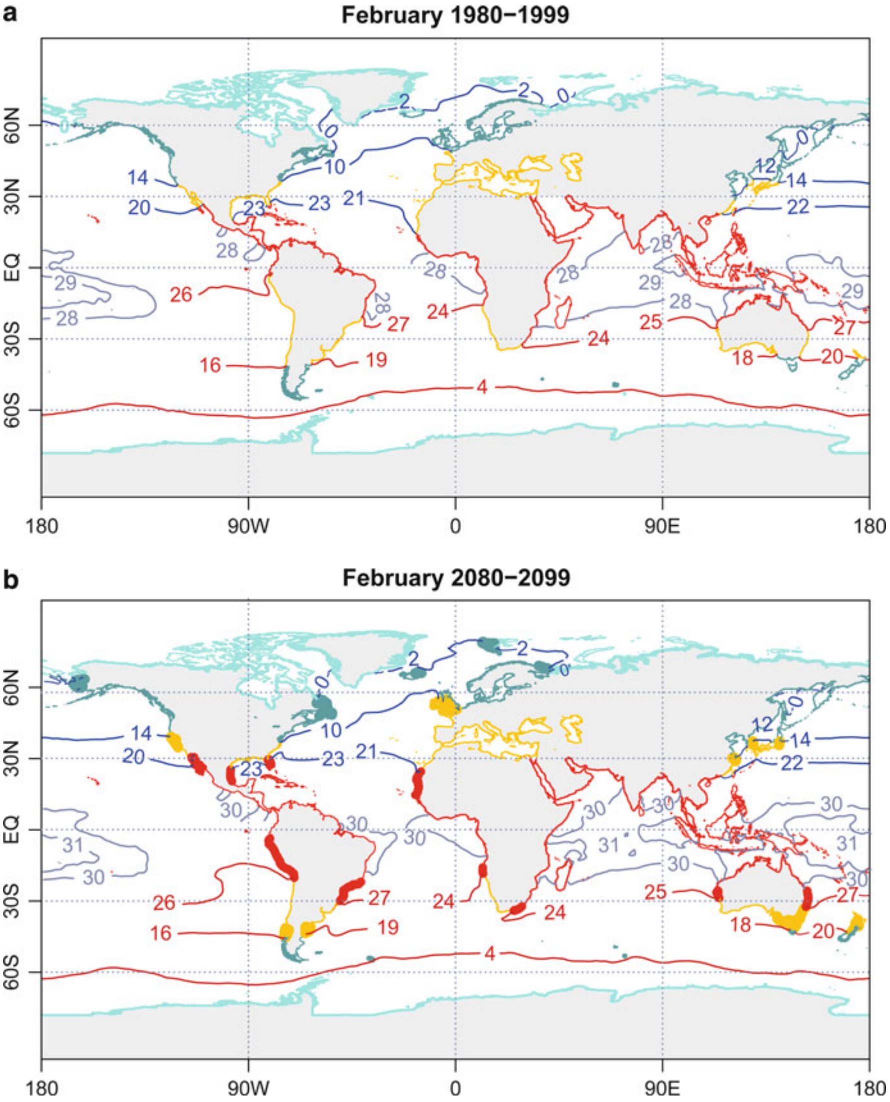

Fig. 18.1 Changes in the extent of biogeographical regions after Briggs (1995) due to global warming at the end of the twentieth century inferred from current (1980–1999) and future (2080–2099) mean February sea surface isotherms. The mean February sea-surface isotherms delimiting current biogeographical regions are depicted in figure **a**. The future extension of the biogeographical regions (**b**) is based on the modeled change of the mean February sea surface isotherms at the present boundaries of the respective regions. Projected changes are indicated by bold coastal lines. Color code of biogeographical regions: *turquoise:* Polar regions, *blue-green*: cold-temperate regions, *yellow*: warm-temperate regions, *red*: tropical regions. Color code of isotherms: *blue*: winter isotherms, *red*: summer isotherms, *gray*: isotherms characterizing the central tropics

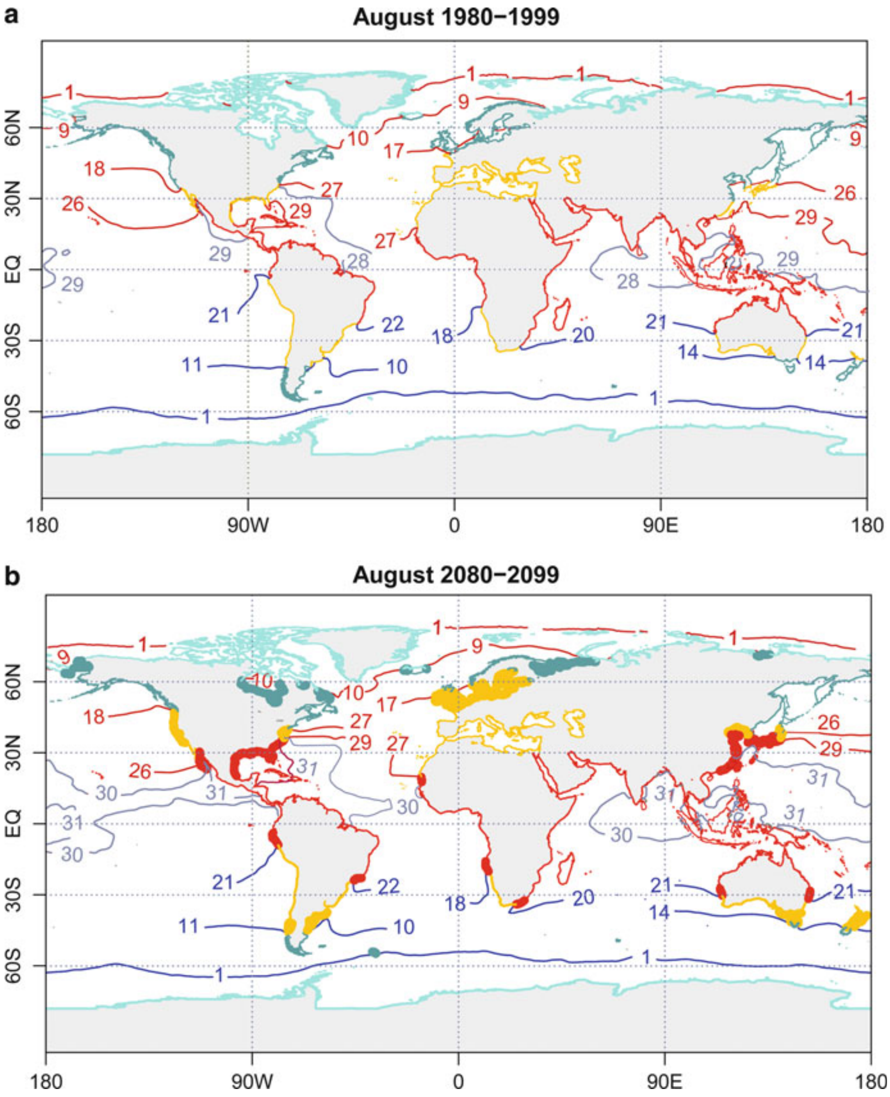

Fig. 18.2 Changes in the extent of biogeographical regions after Briggs (1995) due to global warming at the end of the twentieth century inferred from current (1980–1999) and future (2080–2099) mean August sea surface isotherms. The mean August sea-surface isotherms delimiting current biogeographical regions are depicted in figure **a**. The future extension of the biogeographical regions (**b**) is based on the modeled change of the mean August sea surface isotherms at the present boundaries of the respective regions. Projected changes are indicated by bold coastal lines. Color code of biogeographical regions: *turquoise:* Polar regions, *blue-green*: cold-temperate regions, *yellow*: warm-temperate regions, *red*: tropical regions. Color code of isotherms: *blue*: winter isotherms, *red*: summer isotherms, *gray*: isotherms characterizing the central tropics

and Atlantic compared to the eastern sides of the oceans. The boundary between the warm- and cold-temperate regions is characterized by 16–29°C summer SSTs and by 10–20°C winter SSTs. These extreme differences are attributed to the pronounced compression of isotherms along the western part of the Atlantic and Pacific in contrast to the eastern part of the oceans (see Figs 12.2, 12.3 in Müller et al. 2011). When comparing both hemispheres pronounced differences become apparent as well. The southern boundary of the Arctic region, for example, is described by the 9–10°C summer isotherm, whereas the northern boundary of the Antarctic region is the 4°C summer isotherm (Table 18.1, Figs. 18.1a and 18.2b). The situation in the southern hemisphere might be partially attributed to missing continuous land masses in the circumpolar Southern Ocean. Thus, the limit between the polar and cold-temperate coastal regions in the southern hemisphere is not clearly defined. The largest differences between northern and southern hemispherical biogeographic regions become apparent at the boundary of the warm- and cold-temperate regions at the western coasts of both the Atlantic and the Pacific. In the N-Atlantic, this boundary is situated at the 27°C summer isotherm. In contrast, in the S-Atlantic it is located at the 19°C summer isotherm (Table 18.1, Figs. 18.1a and 18.2a). At the west coasts of the Pacific the differences are smaller (26°C August isotherm in the north to 20°C February isotherm in the south).

18.3 Responses of Seaweeds to Temperature Changes

18.3.1 General Responses

Seaweeds can principally respond to environmental changes in four ways which all may result in distributional and diversity changes: on short timescales, they can acclimate. On medium to long timescales they either adapt to new conditions or are able to slowly migrate keeping pace with the changing environmental pressure. Species unable to acclimate, adapt, or disperse may be captured in isolated refugia or become extinct. Acclimation to temperature stress in seaweeds has been mostly studied on the level of photosynthesis or growth (e.g., Davison et al. 1991; Kübler and Davison 1995; Eggert et al. 2006; see Chap. 3 by Eggert). Locally, the acclimation potential of thermal traits can shape the vertical or seasonal distribution pattern of species (Davison and Pearson 1996; Ateweberhan et al. 2005; Zardi et al. 2011) and on a broader scale eurythermal species have a broader distribution range than stenothermal species (see also Chap. 3 by Eggert). Hitherto, it is unknown whether species with a broad acclimation potential also had or will have a faster genetic adaptation potential—a fact which would help to explain historical or future biogeographical processes.

Adaptive processes on the physiological and molecular level are explained in detail in Chap. 3 by Eggert. On the organism level, the adaptation processes to temperature changes have been identified by comparing the temperature requirements of tropical and cold-water seaweeds from both hemispheres in relation to the climatic history of the various regions (Wiencke et al. 1994). Since Mesozoic times [251–65.5 million years before present (My)] there was a continuous warm water girdle around the earth so that cold-water seaweed species probably only evolved after the glaciation events in the Tertiary (65 My) (Lüning 1990). An upper survival temperature of 33–35°C may still be found in representatives of temperate and tropical seaweed species, indicating that this thermal trait is rather deeply entrenched and not subject to fast adaptation (Lüning 1990). While strictly tropical seaweed species are stenothermal and may survive 30–37°C and grow best between 25 and 30°C, they do not have the ability to live below temperatures of 7–12°C (Pakker et al. 1995; Bischoff-Bäsmann et al. 1997). The first steps in the adaptation of seaweeds to lower temperatures are an increase in cold tolerance and an increase of growth and reproduction rates at lower temperatures leading to eurythermal species. This temperature trait is apparent in tropical to warm-temperate species which acquired a better lower temperature tolerance with survival temperatures between 6 and ≤1°C without losing the upper temperature tolerance (Yarish et al. 1984; Pakker et al. 1995; Bischoff-Bäsmann et al. 1997). Later, the ability to survive temperatures ≥20°C and to grow and reproduce at ≥15–20°C was lost. This type of temperature response is typical for endemic Arctic and Arctic to cold-temperate distributed seaweeds exposed to low temperatures for about 3 My (Briggs 1995). The last steps in the adaptation to low temperatures are the loss of the ability to grow and reproduce at ≥5–10°C and to survive temperatures ≥6–13°C (Wiencke et al. 1994; Bischoff-Bäsmann and Wiencke 1996). This type of temperature response is exemplified in endemic Antarctic species exposed to cold water for at least 14 My (Crame 1993; Briggs 1995). So, the climatic history during species evolution determines the temperature requirements of seaweeds in all biogeographical regions. All these cases give moreover an insight into the time periods needed for adaptation to changing temperatures. Physical barriers and differential environmental gradients along coastlines also may produce ecotypic adaptation. There has been a wealth of studies tackling this question. It became evident that upper tolerance limits seemingly are quite stable within several seaweed species (Lüning 1990 and references therein). True temperature ecotypes have only been found in a few species yet (e.g., *Ectocarpus siliculosus*: Bolton 1983, *Saccharina latissima*: Gerard and Du Bois 1988).

18.3.2 Changes of Seaweed Distribution and Oceanic Temperature in the Geological Past

Interesting examples for migration in the geological past are present-day amphiequatorial species such as *Acrosiphonia arcta* (Chlorophyta) or the species pair *Desmarestia confervoides/D. viridis* (Phaeophyceae), which are absent in the tropics. The fast evolving internal transcribed spacer region of the rDNA of northern and southern hemisphere populations of both entities only exhibit minor variation, suggesting that a migration across the equator took place at the maximum of the Würm/Wisconsin glaciation 18,000 years ago, the so-called last glacial maximum (LGM; van Oppen et al. 1993). The hypothesized migrationist transit of the tropics is supported by the temperature tolerance of both species which is high enough (25°C) to survive a passage through the tropics at the LGM (Peters and Breeman 1992; van Oppen et al. 1994; Bischoff and Wiencke 1995). Similarly it is assumed that a common ancestor of the warm-temperate NE-Atlantic kelp species *Laminaria ochroleuca* and its S-Atlantic sister species *L. abyssalis* and *L. pallida* was able to survive the passage through the tropics during glacial lowering of seawater temperatures by its gametophytic microstages being able to survive at least 25°C (tom Dieck 1992; tom Dieck and de Oliveira 1993).

During the last glaciations, the Arctic ice cap extended south to ~45–55°N and there was a considerable southward shift of the Gulf Stream (CLIMAP Project members 1981; Bradley 1985) inducing major latitudinal dislocations of marine biota in the N-Atlantic between glacial and interglacial periods (van den Hoek and Breeman 1989; Breeman 1990). Some seaweed species were faced with an extreme reduction in their distribution area. The conditions were particularly severe in the NW-Atlantic, where distributions became excessively reduced. A pertinent example is the cold-temperate green alga *Cladophora sericea*. By comparing temperature demands of the species with modeled glacial sea surface isotherms (van den Hoek and Breeman 1989; Cambridge et al. 1990), it became evident that the distribution area of the species was probably very strongly reduced during the LGM in the NW-Atlantic. In the NE-Atlantic, the distribution was shifted from the coasts of Scandinavia, Great Britain, and France to the Iberian Peninsula, Northwest Africa, and even the Mediterranean became hospitable. These proposed migrational shifts during the LGM within the N-Atlantic have been corroborated by recent phylogeographic studies of diverse seaweed species, indicating the English Channel Region as a primary refugium (e.g., Provan et al. 2005) from which species redispersed to their current distributional range.

An example for a probable extinction during the LGM is the current restriction of the kelp species *Laminaria hyperborea* to the NE-Atlantic. The much greater compression of the distribution areas on the NW-Atlantic during the LGM—if compared to the NE-Atlantic coasts—suggests that *L. hyperborea* was not able to survive the inhospitable conditions in the NW-Atlantic during the LGM and became locally extinct (van den Hoek and Breeman 1989). Other kelp species possibly became isolated in cold-water pockets after the LGM. Examples are the deep-water species *L. rodriguezii* (Huvé 1955; Žuljević et al. 2011) or the isolated population of the southern European kelp *L. ochroleuca* in southern Italy (Giaccone 1972). Nowadays both species are only found below the thermocline in selected Mediterranean habitats.

18.3.3 Changes of Oceanic Temperature and Seaweed Distribution in the Future

Following Müller et al. 2009, we analyzed the observed modern (1980–1999; Rayner et al. 2003) and projected end of century (2080–2099) SST distribution for February and August as representatives of summer and winter extreme temperatures. The SST changes are based on the multimodel ensemble mean of coupled climate model simulations prepared for phase 3 of the Coupled Model Intercomparison Project (CMIP3; http://www-pcmdi.llnl.gov) using an emission scenario which assumes a moderate increase of greenhouse gases (SRESA1B) (for details, see Müller et al. 2009). Both the global mean February and August SSTs are projected to warm by 1.9°C until the end of the century (Fig. 18.3). The maximum

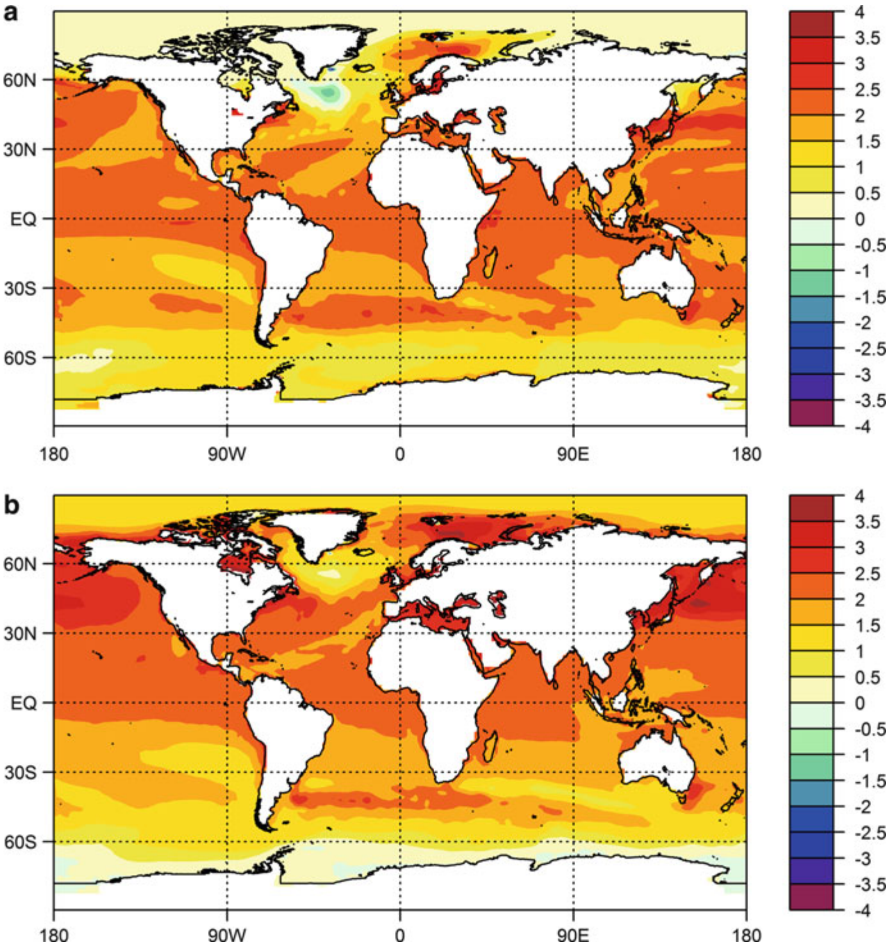

Fig. 18.3 Simulated future changes in sea surface temperature. The ensemble mean anomaly for 2080–2099 relative to 1980–1999 is shown for February (**a**) and August (**b**)

warming of around 4°C is predicted for high latitudes of the northern hemisphere in summer. The larger land area in the northern hemisphere leads to a stronger response to the radiative forcing than in the southern hemisphere. Additionally, the decrease in summer sea-ice cover amplifies the summer warming. In contrast, minimum warming is predicted in the Southern ocean due to strong ocean heat uptake in this region. In addition to this global scale pattern, some regional scale patterns in the temperature changes become visible. As most climate models predict a reduction in the thermohaline circulation as a response to the increasing greenhouse gas concentration, the heat transport from the tropics to the Polar regions will be affected in the northern hemisphere (Schmittner et al. 2005). This will result in a local cooling in the Labrador Sea in winter and a reduced warming in summer according to the model simulations (Fig. 18.3).

The simulated future changes in sea surface temperatures shown in Fig. 18.3 will result in a general poleward movement of biogeographical regions (see Sect. 18.2) until the end of the twentieth century. The extent of the present-day biogeographical regions and the resulting future changes are shown in Figs. 18.1 and 18.2. This projection is based on the location of modeled mean winter and summer sea surface isotherms for the end of the twentieth century (Müller et al. 2009, Appendix Figs. 1 and 2) characteristic for the current boundaries of the respective regions (see Table 18.1, Figs. 18.1a and 18.2a). Despite the proven recent regional warming in the western Antarctic Peninsula (Vaughan et al. 2003) there will be almost no changes in the northern delimitation of the Antarctic region until the end of this century based on our model. The Arctic region, in contrast, will shrink considerably at its southern border, especially due to warmer winter temperatures while new ice-free coastal Arctic habitats will become available in the north following the retreating pack-ice border (1°C August isotherm) in summer (Fig. 18.2b; Müller et al. 2009). The current cold-temperate regions of both hemispheres will become compressed as the warm-temperate regions are shifting polewards. The cold-temperate regions will gain much new area at the expense of the Polar region only in the N-Atlantic while in the S-Atlantic only the small sub-Antarctic islands will become cold-temperate. The poleward expansion of the warm-temperate regions at the expense of the cold-temperate regions is especially evident in western and eastern S-America, in southeastern Australia and New Zealand, western N-America, and along the European coastline. The warm-temperate regions themselves will lose habitats at the expense of the projected widening of the tropical regions (Figs. 18.1 and 18.2). Recently, it was shown that this process has already started and five different types of climatological measurements revealed a widening of the tropical region of several degrees latitude since 1979 (Seidel et al. 2008). According to our results, this future widening will be especially pronounced along the west and east coast of S-America, along the northern and eastern coastlines of S-Africa and Australia, in SE-Asia, W-Africa, and the Gulf of Mexico (Figs. 18.1 and 18.2).

It becomes apparent that the location of the boundary isotherms characterizing present-day biogeographical regions (Table 18.1) will not move polewards at the same pace according to the model simulations (Figs. 18.1 and 18.2). Thereby, the annual mean temperature minima and maxima and the resulting temperature gradient will change along vast coastlines compared to present day. As a consequence, some biogeographical regions will not be extended or reduced as a whole

(Figs. 18.1 and 18.2). Two examples shall demonstrate resulting consequences. Along the coast of China and Japan tropical winter temperatures will not change in the future so that the 22°C February isotherm will stay at approx. 23°N (Fig. 18.1b). In contrast, the corresponding 29°C summer isotherm characterizing the warm-temperate/tropical boundary nowadays will move from approx. 23°N up to the Yellow Sea and Strait of Korea to approx. 36°N (Fig. 18.2b). Hence, this whole area will become a transitional region where biota will experience a reorganization according to the individual growth, reproduction, and lethal limits of the species present (van den Hoek 1982a, b; see Chap. 3 by Eggert). These temperature changes will probably also have consequences for the intensive seaweed aquaculture industry along the Chinese and Japanese coastlines (see Chap. 22 by Buchholz et al.). Another prominent example of a future transitional region is the west coast of S-America. The current austral 21°C winter and 26°C summer SST delimit the biogeographical boundary between the warm-temperate and tropical regions approx. at a latitude of 5°S (northern Peru). According to our simulations, both isotherms will move southwards to approx. 10°S in future austral winter or to approx. 20°S (northern Chile) in future austral summer. The difference between the current and future boundary region thereby spans either 5° or 15° latitude (Figs. 18.1 and 18.2). Thus, a coastline of more than 1,000 km length will become a biogeographical transition region and composition of biota will probably change. It should be noted, however, that due to the influence of the cold Humboldt current and coastal upwelling regions in general, biogeographical regions may not always correspond to the system developed by Briggs (1995) and the model assumptions. Recent evidence, for example, suggests that the northern boundary of the cold-temperate region along the western coastline of S-America set to approx. 40°S by Briggs (1995) actually extends further north to approx. 30°S (Camus 2001; see also Chap. 14 by Huovinen and Gómez).

In addition, the model data identify areas where winter and summer isotherms and thereby possibly the whole biogeographical region will shift homogenously. Examples are the warm-temperate region in eastern and western S-America or the tropical region along eastern and western southern Africa (Figs. 18.1b and 18.2b). Although it is not yet predictable whether minimal and maximal or mean annual SST or altogether will be most responsible for shaping future phytogeographical regions, our data obviously show that new correlations of biogeographical regions with SSTs will establish.

18.3.4 Specific Effects of Oceanic Warming on Seaweed Distribution and Ecology

18.3.4.1 Polar Regions

Since the late 1970s the glacial ice sheets have retreated by up to 2% per decade (Serreze et al. 2007) and the Arctic will probably be ice free by the end of this century (Johannessen et al. 2004). In the Antarctic, 87% of the glaciers of the West Antarctic Peninsula are retreating (Cook et al. 2005), the ice season has shortened by about 90 days, and perennial ice does not occur any more at this location (Martinson et al. 2008; Stammerjohn et al. 2008). In the Arctic, oceanic warming leads to a retreat of the pack-ice border coinciding with the 1°C summer isotherm. This will provide new habitats for algal colonization in the Arctic and Antarctic along rocky coastlines (Fig. 18.1; Müller et al. 2009, 2011). As ice-related pressures on shallow water biota of the Arctic and Antarctic will be reduced, perennial macroalgae, which are so far restricted mainly to the sublittoral, will be able to colonize the eulittoral, resulting in an increase in biomass and diversity (Weslawski et al. 2010, 2011). On the other hand, prolonged inflow of glacial melt water will reduce salinity and increase turbidity of the water due to a higher sediment impact (Campana et al. 2011). The concomitant reduction of the euphotic region will change production rates (Pivovarov et al. 2003; Deregibus et al. personal communication; Spurkland and Iken 2011) and probably will cause an upward shift of the depth limit of seaweeds. Biomass and seaweed cover already increased between 1988 and 2008 in the rocky littoral of Sorkappland (Svalbard; Weslawski et al. 2010) in the Arctic accompanied by an increase in air temperature and SST and a marked decrease in the duration and extent of sea-ice cover. However, no "new" species were detected but are expected in future (Müller et al. 2009). The described upward shift of seaweeds might though be counteracted by high levels of ultraviolet-B radiation (UVBR) due to stratospheric ozone depletion (Weatherhead and Andersen 2006; Zacher et al. 2011) which still prevails in the Arctic and Antarctica. UVBR is one of the most important factors controlling the upper depth distribution of seaweeds. Effects have been demonstrated from the cellular to the ecosystem level, affecting community structure and diversity in the Arctic and Antarctic (Bischof et al. 2006; Zacher et al. 2007; Campana et al. 2011; Karsten et al. 2011; Fricke et al. 2011; see Chap. 20 by Bischof and Steinhoff). UVBR, turbidity, water temperature, and sea-ice conditions are interdependent factors but multifactorial interactive effects on polar biota have scarcely been investigated (Müller et al. 2008; Fredersdorf et al. 2009). Bifactorial experiments on Arctic kelp species indicated that negative effects of UVBR can be mitigated by the interaction with increased temperature. For example, germination of zoospores of the kelp *Laminaria digitata* was inhibited almost completely by UVBR at 2°C, but not at 7°C (Müller et al. 2008).

Compared to changes in the Arctic, the distributional changes of seaweeds in the Antarctic will probably be minor (Müller et al. 2009, 2011) as the model data predict an SST increase of only 1°C throughout the year in the Antarctic region. Moreover, only few cold-temperate species will be able to colonize present-day Antarctic coasts. One example might be the brown alga *Chordaria linearis*, which has been found already on two locations in West Antarctica (Müller et al. 2009, 2011). The estimation of minor changes for seaweed richness along the coastal West Antarctica Peninsula under climate change conditions contrasts to demonstrated changes in the respective pelagic ecosystem in response to rapid climate changes, which include a shift in phytoplankton biomass, in zooplankton community structure, and expected effects on higher trophic levels (Schofield et al. 2010).

18.3.4.2 Temperate Regions

Within the last decades, an increase in SSTs of >2°C has been documented in many cold- and warm-temperate regions (see Sect. 18.1). At many temperate European coastlines, migrational shifts of benthic and pelagial species have already taken place (e.g., benthos overview: Mieszkowska et al. 2006; Hawkins et al. 2008; plankton: Beaugrand and Reid 2003; fish: Rijnsdorp et al. 2009). Climate driven biomass changes or loss of kelp vegetation has recently been reported from many local sites worldwide (e.g., Japan: Kirihara et al. 2006, Tasmania: Johnson et al. 2011, Norway: Andersen et al. 2011, Spain: Díez et al. 2012). In contrast, no evidence for broadscale latitudinal shifts of kelps since 1850 was found in the transition region between the boreal and sub-arctic region in the NW-Atlantic (Merzouk and Johnson 2011). A recent investigation into the decline of the sugar kelp *Saccharina latissima* along southern Norwegian shorelines (Andersen et al. 2011) provides a good example for the complex interactions in the field. After transplantation of *S. latissima* from healthy to impacted sites, normal growth and maturation took place in winter and spring, but heavy fouling of epiphytes occurred over summer followed by mortality. Although duration of periods with summer temperatures >20°C increased in recent years, a temperature which is sublethal for *S. latissima* (Bolton and Lüning 1982), mortality could not unequivocally be correlated to high summer temperatures alone. Instead, Andersen et al. (2011) assumed a cascade of reduced growth at sublethal temperatures, followed by heavy epiphytism at locations with low wave activity leading to shading, thereby causing a negative carbon balance and brittleness of thalli and finally mortality—all factors together possibly preventing recruitment and recovery of the species at the impacted sites. Successful recruitment is crucial for the continuous recovery of boundary populations which becomes impacted if the environmental pressure surpasses critical limits. Within a few years of unfavorable abiotic conditions, the reproductive capacity was dramatically reduced in southern European marginal populations of the intertidal brown alga *Fucus serratus* (Viejo et al. 2011). Similarly, along the SST gradient in western Australia density of kelp recruits was inversely related to increasing mean ocean temperature, suggesting an effect of temperatures on either reproduction or recruits (Wernberg et al. 2010).

There are a few long-term case studies from temperate coastal regions investigating possible ecological consequences of environmental warming for rocky shore communities. Three examples are given here. A 10-year thermal outfall of a power station which induced a long-lasting SST increase by up to 3.5°C resulted in a complete change of the intertidal rocky shore community structure at Diablo Potter Cove in California. The initial dense cover of foliose algae was replaced by bare rocks, algal crusts, or turf algae and there was a major replacement of species and decrease of algal richness (Schiel et al. 2004). A mean SST increase of 0.79°C in the intertidal of Monterey Bay California between 1931 and 1996 led to a significant increase in southern species and a decrease of northern species (Sagarin et al. 1999). In the northern Baltic, another monitoring study of long-lasting warming in the sea (up to 10°C) diminished ice cover and thereby increased light availability in winter. The situation also caused major changes in the quantitative composition of species over the seasonal cycle. While growth of cyanobacteria was promoted and red and brown algae decreased in abundance or disappeared over summer, the latter had a prolonged growth season in autumn and winter due to "better" winter temperatures. Generally, a species-specific response was evident (Snoeijs and Prentice 1989). In future, we expect similar transitional changes in rocky shore communities along all warm- and cold-temperate shorelines possibly subjected to change according to our model results (Figs. 18.1 and 18.2).

18.3.4.3 Tropical Regions

Many coastal hard-bottom tropical and subtropical regions are characterized by coral reefs which also inherit a high seaweed species richness (Diaz-Pulido et al. 2007). The abundance of macroalgae in reefs has been thought to be generally low and controlled by grazing pressure of herbivorous fish (e.g., Wanders 1977; Carpenter 1986; Hay 1997, see Chap. 16 by Mejia et al.). Only in recent years, it was realized that tropical reefs are also algal reefs and a high coverage of macroalgae among corals and natural variability of seaweed abundance on coral reefs is not necessarily indicative of environmental degradation (Vroom et al. 2006, 2010; Vroom and Timmers 2009). Coral–algal interactions are manifold and it is known that algae may inhibit or kill corals (e.g., Titlyanov et al. 2007; Rasher et al. 2011) and vice versa dead corals may negatively influence macroalgal growth (Liu et al. 2009).

As tropical corals and seaweeds are currently living near to their lethal limit, a slight temperature increase of 1–2°C above the mean summer temperatures as predicted for the end of the twentieth century (Fig. 18.3) may already lead to catastrophic events. Coral reefs worldwide have faced severe damage by periodic heat waves especially through extreme ENSO activities since the 1980s inducing so-called coral bleaching events which involve the loss of the symbiotic zooxanthellae after thermal stress (Jokiel and Coles 1990). Baker et al. (2008) describe in their extensive review all facets of this phenomenon. There is a correlation between coral bleaching with maximum monthly SSTs (Manzello et al. 2007). Temperature thresholds for coral bleaching are not uniform but site specific and range from 27.5 to 32°C (Baker et al. 2008). Thereby, they are generally above current mean tropical summer SST of 27–29°C (Fig. 18.2a; Müller et al. 2009, Appendix Figs. 1 and 2), but this will change in future when this region will experience an unprecedented warming (Solomon et al. 2007) with annual mean SSTs of 30–31°C over wide areas (Fig. 18.2b). A possible acclimation of corals to increased temperatures has been observed in the Great Barrier Reef as threshold temperatures increased over time (Berkelmans 2009) and up to now no coral species became extinct. Currently, reefs are still able to recuperate with highly variable rates, indicating a differential recovery capacity. But full recovery of reefs after thermal stress probably needs decades to centuries (Baker et al. 2008). As growth of macroalgae is much faster and their temperature tolerance is several degree Celsius higher than those of corals (Pakker et al. 1995; Bischoff-Bäsmann et al. 1997), a shift from coral to seaweed dominated coastal ecosystems has been proposed for future tropical areas (Hoegh-Guldberg et al. 2007) and has already been observed during recent decades (Rasher et al. 2011 and references therein).

Current warm-temperate coastlines which will become tropical in future (Figs. 18.1 and 18.2) will not be able to compensate for the prospected loss of reefs as rates needed to establish coral reefs are slow (Baker et al. 2008). Similarly as corals, subtidal reef macroalgae potentially face local extinction if temperature exceeds algal tolerance limits which are firmly set to 30–33°C (Pakker et al. 1995). In contrast, eulittoral tropical macroalgae with their higher lethal temperature limits of up 32–37°C (Bischoff-Bäsmann et al. 1997) will be better able to withstand future temperature increase in the central tropics. First local extinctions after warming events have been recorded: In the Galapagos Archipelago six tropical macroalgal species disappeared after the ENSO warming event in 1982/1983. Here a transition of the macroalgal and coral habitats to heavily grazed reefs dominated by crustose coralline "urchin barrens" was observed (Edgar et al. 2010). Additionally to ocean warming, ocean acidification may decrease coralline abundance in future which will enhance the cascade effect of decreasing coral recruitment, opening space for turf algal species, and further inhibition of coral recruitment, coral fecundity, and coral growth (Hoegh-Guldberg et al. 2007). Unfortunately, the functional ecology and thermal traits of coralline red algae which are important contributors to reef structure and facilitate settlement of corals are virtually unknown (Nelson 2009).

As the tropical region will considerably extend polewards at the expense of the current warm-temperate region (Figs. 18.1 and 18.2), substantial new transitional areas will develop along rocky shore coastlines characterized, for example, by assemblages dominated by tropical to subtropical members of the brown algal order Dictyotales and not corals such as described for tropical to warm-temperate transitional areas of the Canary Islands (Sangil et al. 2011). Locally, other factors such as wave exposure, local currents, and physical barriers may be more important than temperature for biogeographic distribution as has been observed along a tropical to warm-temperate coastal transition region in E-Australia where species distribution is still stable despite recent rapid warming (Poloczanska et al. 2011).

18.4 Assumptions for Global Seaweed Biodiversity

Global patterns of marine diversity differ from terrestrial habitats where species numbers decrease moving away from the equator in both hemispheres (Pianka 1966; Willig et al. 2003). Marine coastal taxa also show clear latitudinal trends, but overall seaweed genus diversity peaks in mid latitudes and not the tropical region (Kerswell 2006; Santelices et al. 2009; Tittensor et al. 2010). SST was identified as one significant predictor of overall coastal species richness (Tittensor et al. 2010) and high interannual temperature variability was proposed as explanation for the depauperate brown algal flora along the southwest African and north-central Chilean coastline (Bolton 1996). Thus, the predicted changes in SST for the end of the twentieth century will probably have a substantial effect not only on distribution of seaweeds and marine communities in general, but also on global marine diversity. Kerswell (2006) analyzed the latitudinal pattern of global seaweed genus diversity and seaweed endemism in detail. As in other coastal taxonomic groups (Tittensor et al. 2010) there is a band of high diversity in the northwestern Pacific surrounding the Japanese archipelago and in the southwestern Pacific along the southern Australian coastline (Kerswell 2006). In the Atlantic, there is a major hotspot of diversity along the European coastline (Kerswell 2006). All these regions inherit a high seaweed genus diversity and have been identified by our model data to be impacted by future warming. Thus, major changes in seaweed species richness, and the functionality of assemblages through species extinctions, species invasions, and changes in trophic relationships (Sala and Knowlton 2006) are expected especially in these regions. Within the last decade, a wealth of cryptic seaweed species has been described with the help of modern molecular biological tools (e.g., van der Strate et al. 2002; Brodie et al. 2007; Verbruggen et al. 2009). Thus, species richness of marine algae and genetic diversity of their populations probably is strongly underestimated (Zuccarello et al. 2011) and thereby possibly also their adaptive potential to change. But it is not yet clear whether genetic differentiation always coincides with ecological differentiation (Tronholm et al. 2010).

18.5 Synopsis

Clearly, the prospected worldwide changes in SSTs will exert a differential pressure on seaweed species and assemblages along biogeographical regions. As the ice-free Arctic coastlines and all other regions will expand polewards, the tropical biogeographical region will widen considerably. In contrast, there will be almost no change in the northern limit of the Antarctic region. Most effects on biota will be expected in biogeographical transition regions which have been identified here, for example along the warm- to cold-temperate European coastline or along the warm-temperate to tropical coasts of SW and SE-America, Japan, or China. In these areas, summer and winter SST will move polewards with a differential magnitude so that annual temperature gradients will become more pronounced in some areas. Hence, severe biotic changes are expected as the assemblages characterizing the biogeographic regions will not be able to shift as a whole. Rather, we predict differential species-specific shifts depending on the respective temperature-dependent life cycle characteristics of species which additionally will be shaped by other abiotic and biotic factors. Comparison of coastal areas comprising present-day highest seaweed genus diversity with future biogeographical transition areas revealed a correlation in some cases, for example along western European, Japanese, or southern Australian shorelines. In the future, it will be particularly interesting to investigate the changing structure and function in these transitional biogeographical regions to gain a better understanding of fast acclimation and adaptation rates on an ecosystem level.

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Chapter 19
Seaweed Responses to Ocean Acidification

Michael Y. Roleda and Catriona L. Hurd

19.1 Introduction

Since the start of the industrial revolution (~1850), burning fossil fuels, cement manufacturing, and changes to land use have increased atmospheric carbon dioxide (CO_2) concentrations from ~280 to 385 ppm. For the coming decades, the 2007 IPCC report on climate change predicts a continued rapid rise in atmospheric CO_2 leading to significant temperature increases in the atmosphere and ocean (IPCC 2007). Another consequence of increasing anthropogenic CO_2 is a reduction in the pH of the world's ocean and concomitant changes in seawater carbonate chemistry, termed ocean acidification. Ocean acidification (OA) may have profound impact on biogeochemical cycles, marine organisms, ecosystems, and the services they provide. In combination with warming seas and other stress factors (e.g., eutrophication, UVR), this will create multiple threats to the marine environment. This chapter will discuss seawater chemistry and algal carbon physiology, and concentrate on seaweed responses to OA by themselves and in synergy with other environmental stresses. Reference to phytoplankton, seagrasses, and corals is made where appropriate.

19.2 Anthropogenic CO_2 and Seawater Carbonate Chemistry

The world's oceans have taken up ~30% of anthropogenic CO_2 and have buffered climate change in terrestrial systems by reducing the atmospheric concentration of this greenhouse gas (Feely et al. 2004). The air–sea gas exchange equilibrates surface seawater CO_2 to atmospheric levels with a timescale of ~1 year (Doney

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Table 19.1 Average changes to ocean chemistry and pH based on ocean carbon models and surface-ocean measurements (modified from The Royal Society 2005)

	Preindustrial	Today	2× preindustrial	3× preindustrial	4× preindustrial
CO_{2atm} (ppm)	280	380	560	840	1,120
H_2CO_3 (μmol kg^{-1})	9	13	19	28	38
HCO_3^- (μmol kg^{-1})	1,768	1,867	1,976	2,070	2,123
CO_3^{2-} (μmol kg^{-1})	225	185	141	103	81
Total DIC (μmol kg^{-1})	2,003	2,065	2,136	2,201	2,242
Mean surface pH	8.18	8.07	7.92	7.77	7.65
$\Omega_{calcite}$	5.3	4.4	3.3	2.4	1.9
$\Omega_{aragonite}$	3.4	2.8	2.1	1.6	1.2

et al. 2009), and the seawater carbonate chemistry is governed by a series of chemical reactions that are in equilibrium (see also Chap. 2 by Gómez and Huovinen and Chap. 4 by Gordillo):

$$CO_{2(atoms)} \leftrightarrow CO_{2(aq)} + H_2O \leftrightarrow H_2CO_3 \leftrightarrow H^+ + HCO_3{}^- \leftrightarrow 2H^+ + CO_3^{2-}$$

CO_2 reacts with H_2O causing the equilibrium to shift such that the concentration of the bicarbonate ion (HCO_3^-) and carbonic acid (H_2CO_3) increases, while that of carbonate ions (CO_3^{2-}) declines. The increase in hydrogen ion concentration lowers pH because pH $= -\log_{10}[H^+]$. The mean surface ocean pH has already decreased by 0.1 unit (equivalent to a 30% increase in H^+) from ~8.18 at the beginning of the industrial revolution. For surface seawater with pH of ~8.07, approximately 91% of the inorganic carbon is HCO_3^-, 8% CO_3^{2-}, and only 1% $CO_{2(aq)}$. By 2100, concentrations of $CO_{2(aq)}$ and HCO_3^- are predicted to increase by 192% and 14%, respectively, and CO_3^{2-} decrease by 56%, with a concomitant decline in pH to 7.65 (The Royal Society 2005). Aside from the decline in carbonate concentration, a reduction in the saturation state of aragonite and calcite is also predicted (Table 19.1). As the seawater saturation state for a mineral measures its thermodynamic potential to form or to dissolve, a reduction will make calcified structures more vulnerable to erosion.

Carbonate ions play an important role in the formation of calcareous "skeletons" for a large number of phototrophic marine organisms including corals, phytoplankton, and macroalgae. If mitigation of emissions does not occur, CO_2 concentrations could reach >800 ppm by 2100 that could result in a decrease of ~0.4 pH units. Under a worst-case scenario of continued and unabated usage of known fossil fuel reserves, modeling indicates that average surface ocean pH could fall by a maximum of 0.77 pH units by 2300 (Caldeira and Wickett 2003). Marine organisms would then experience the lowest pH level for ~20 million years and the most rapid rate of decline in pH ever (Turley 2008). While the OA event experienced 55 million years ago during the Paleocene–Eocene thermal maximum probably occurred over several thousand years, the present-day anthropogenically induced event is happening over decades to centuries (Zachos et al. 2005).

In 2005, a Royal Society Report highlighted the potential effects of OA on marine organisms. Initial research has focused on how the lowered availability of carbonate ions might impact marine calcifiers, particularly corals, calcareous micro- and macroalgae, and other shell-forming invertebrates. However, because the relative availability of CO_2 and HCO_3^- will also change and algae use one or both of these as a CO_2 source for photosynthesis, OA has the potential to affect the rates of photosynthesis, and hence growth and productivity, of all algae.

19.3 Carbon Sources and Acquisition

In seawater, there are two sources of inorganic carbon (C_i: also known as Dissolved Inorganic Carbon, DIC, and Total Inorganic Carbon, C_T) to seaweeds, HCO_3^-, which is available in high concentrations (2,200 μM), and CO_2 (14 μM). Most seaweeds are able to take up HCO_3^- and/or CO_2 by active transport (termed a carbon concentrating mechanism, CCM), while some seaweeds (mostly reds) rely on CO_2 uptake by passive diffusion (Hurd et al. 2009; see also Chap. 2 by Gómez and Huovinen and Chap. 4 by Gordillo).

The enzyme carbonic anhydrase (carbonate dehydrase) EC 4.2.1.1 (CA) catalyses the reversible hydration of CO_2 and is widely distributed not only in plants but also in animals and prokaryotes. CA is synthesized within the cytoplasm but may also be found associated with the chloroplast. They are also found on the plasmalemma, where they have access to the external medium (Giordano and Maberly 1989). Although the significance of CA is not yet fully understood, it is generally believed to play a role in carbon acquisition and photosynthesis, where high CA activity is correlated to aquatic plant's ability to concentrate CO_2 internally in response to low CO_2 concentrations in the growth medium.

Inorganic carbon concentrating mechanisms (CCMs) cause the accumulation of CO_2 around RUBISCO (ribulose-1,5-bisphosphate carboxylase oxygenase) in organisms capable of oxygenic photosynthesis (e.g., all cyanobacteria, most algae and aquatic plants, and in C_4 and crassulacean acid metabolism (CAM) of vascular plants). In algae, CCMs are polyphyletic (more than one evolutionary origin) and involve active transport of HCO_3^-, CO_2, and/or H^+, or an energized biochemical mechanism similar to C_4 and CAM plants (Raven et al. 2008). CCMs involve both the active transport of HCO_3^- and/or CO_2 and the catalytic conversion of HCO_3^- to CO_2 with subsequent passive diffusion of CO_2. CCMs effectively alleviate the low CO_2 affinity of the enzyme RUBISCO which is less than half saturated under current dissolved CO_2 concentrations [$CO_{2(aq)}$]. Different types of CCM are present in different phototrophs (Table 1 in Giordano et al. 2005) and different models for inorganic carbon transport and CCM are schematized in cyanobacteria (Fig. 1 in Giordano et al. 2005) and eukaryotic algae (Figs. 1 and 2 in Thoms et al. 2001, and Moroney and Ynalvez 2007; Fig. 1 in Giordano et al. 2005). While pyrenoids in eukaryotic algae play an important role in CCMs (Badger et al. 1998), their absence does not necessarily imply the absence of a CCM (e.g., *Caulerpa scalpelliformis*, Kevekordes et al. 2006).

A number of seaweeds lack a CCM and rely solely on CO_2 diffusion from the external environment (Raven et al. 2005). In order to carry out net C assimilation under current CO_2 and O_2 levels, RUBISCO of the organism should have high selectivity factor (S_{rel}) that defines the relative rates of carboxylase and oxygenase reactions to diffusive CO_2 supply (Giordano et al. 2005). Macroalgae lacking CCMs are often found inhabiting fast-flow environments, to minimize the diffusion boundary-layer thickness (see Sect. 19.7.1), or in deep water with low light levels where a smaller CO_2 flux is required to satisfy cellular assimilatory requirements (Sherlock and Raven 2001; Raven et al. 2002a, b; Hepburn et al. 2011). Oxygenic photolithotrophs have a diversity of incompletely understood mechanisms of inorganic carbon acquisition that require further studies. Raven (2010) recommended four areas of research where more studies are needed: (1) Diffusive CO_2 entry, where a number of algae are, in various respects, intermediate between diffusive CO_2 entry and occurrence of a CCM, (2) the nature and role of cyanelles (plastids) in organic carbon assimilation, (3) the energetics of CCM in *Chlamydomonas reinhardtii*, the eukaryotic alga with the best understood CCM, and (4) the occurrence of C_4-like metabolism in the CCMs of marine diatoms.

Methods used to determine whether an alga is a HCO_3^- or CO_2 user include: (1) pH drift experiments, with HCO_3^--using algae being capable of raising pH of the surrounding medium to values in excess of those attained by species using only CO_2, (2) pH dependence of half saturation constants, $K_{0.5}$ (HCO_3^-) or $K_{0.5}$ (CO_2), (3) HCO_3^- utilization pathway inhibitors, (4) isotope disequilibrium, and (5) membrane-inlet mass spectroscopy (Giordano et al. 2005). Aspects of inorganic carbon acquisition, metabolism, and carbon isotope discrimination by marine macroalgae are discussed by Kremer (1981), Johnston (1991), Maberly et al. (1992), and Raven et al. (2002b).

Applying one or a combination of these various techniques shows that most algae examined can take up both HCO_3^- and CO_2. However, there is some evidence that some algae can take up only CO_2 while other species can only actively transport HCO_3^-. Using the natural abundance of $^{13}C/^{12}C$ ratios (as $\delta^{13}C$) as a proxy, marine macroalgae with $\delta^{13}C$ values lower than –30‰ rely on diffusive CO_2 supply to RUBISCO (Maberly et al. 1992) while organisms with $\delta^{13}C$ higher than –10‰ (a value more positive than $\delta^{13}C$ of CO_2 in seawater) must involve HCO_3^- use (Raven et al. 2002b). In combination with pH drift experiments, HCO_3^--using macroalgae can shift seawater pH to 9.0 or higher (Maberly 1990) and have corresponding $\delta^{13}C$ values less negative than −30‰. Conversely, CO_2-using species have $\delta^{13}C$ values more negative than −30‰ and were unable to raise pH above a critical value of pH 9 (Maberly et al. 1992).

The expression Δ which represents the $\delta^{13}C$ value of the algal sample ($\delta^{13}C_{alga}$) relative to the $\delta^{13}C$ of the source of inorganic carbon used in photosynthesis ($\delta^{13}C_{CO_2}$), is also indicative of certain photosynthetic pathways. Previous work strongly suggests that Δ values in excess of 20‰ are associated with diffusive CO_2 entry and C_3 pathway of CO_2 fixation while Δ values below 20‰ are consistent with HCO_3^- use and CO_2 uptake by a nondiffusive mechanism (Raven et al. 1995 and references therein). A correlation was found between the two proxies for

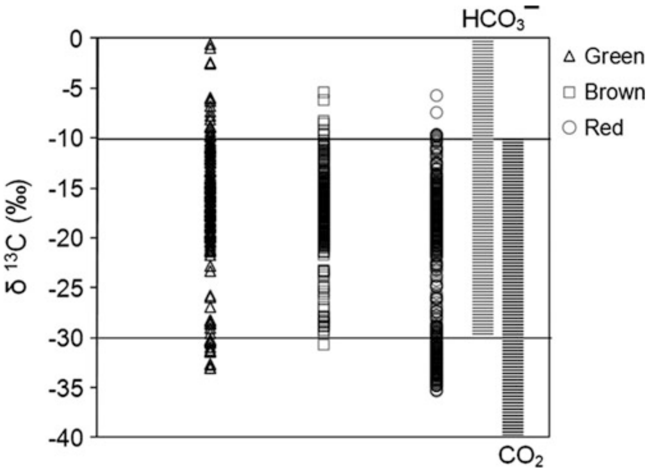

Fig. 19.1 $\delta^{13}C$ signatures of different macroalgae as a proxy of their carbon use strategy ($n = 857$, representing 370 species sampled from ten thermographic regions described by Adey and Steneck 2001). *Horizontal lines and bars* to the right delimit the range of possible values for species restricted wholly to CO_2 or HCO_3^- (see text and cf Maberly et al. 1992). The sources of data used here are Black and Bender (1976), Bode et al. (2006), Corbisier et al. (2006), Dunton (2001), Fischer and Wiecke (1992), Kang et al. (2008), Kevekordes et al. (2006), Kübler and Raven (1994), Laurand and Riera (2006), Maberly et al. (1992), Pinnegar and Polunin (2000), Raven et al. (1995, 2002b), Runcie et al. (2008; unidentified Corallinales not included), Vizzini and Mazzola (2006), Wang and Yeh (2003), and Wozniak et al. (2006)

diffusive CO_2 uptake where macroalgae with $\delta^{13}C$ more negative than –30‰ also have Δ above 20‰ (Raven et al. 1995; Runcie et al. 2008). Several conditions of using stable isotopes to describe the carbon physiology of macroalgae are discussed by Raven et al. (2002b).

Using pH drift experiments and carbonic anhydrase activity measurements, the preference of different macroalgae for either CO_2 or HCO_3^- or both as source of inorganic carbon has previously been compiled and reviewed (Table 3 in Gao and McKinley 1994 and references therein). For example, pH drift measurements showed that the brown alga *Carpophyllum* sp. most likely uses CO_2 rather than HCO_3^- (Dromgoole 1978). On the other hand, using $\delta^{13}C$ data in the literature as a proxy for carbon use, the values for seaweeds (Fig. 19.1) vary from –0.64‰ for *Halimeda distorta* (Chlorophyta: Bryopsidophyceae) collected from 99 m depth at Penguin Bank off the island of Moloka'i, Hawaii archipelago (Runcie et al. 2008) to −35.3‰ for *Georgiella confluens* (Rhodophyta: Floridiophyceae) from Anvers Island off the Antarctic Peninsula (Dunton 2001). Most seaweeds have $\delta^{13}C$ between −30 and −10‰, within the range in which both CO_2 and HCO_3^- use can occur (Maberly et al. 1992; Raven et al. 1995). Macroalgae that rely solely on HCO_3^- as carbon source ($\delta^{13}C > -10‰$) are 10 greens, 5 browns, and 6 reds while macroalgae that depend on CO_2 diffusion ($\delta^{13}C <$ –30‰) consist of 6 greens, 1 brown, and 51 reds. Most of these CO_2-using deep water red macroalgae belongs to the Class Florideophyceae (94%), with 51% from the Order Ceramiales, 18% Plocamiales, and 14% Gigartinales. The green CO_2-using macroalgae are different species of *Caulerpa* and *Udotea petiolata* (Raven et al 2002b; Kevekordes et al. 2006; Vizzini and Mazzola 2006). The $\delta^{13}C$ signature of the brown macroalga *Desmarestia anceps* is inconclusive with values ranging from −25.3‰ (Dunton 2001) to −30.68‰ (Fischer and Wiecke 1992). Inconclusive values are also observed in six red macroalgae, *Lomentaria articulata, Membranoptera alata, Odonthalia dentata, Palmaria decipiens, Ptilota gunneri*, and *Trailliella intricata* (Fischer and Wiencke 1992; Kübler and Raven 1994; Maberly et al. 1992; Raven et al. 2002b) and in the green macroalga *Caulerpa obscura* (Raven et al. 2002b). On the other side of the spectrum, inconclusive $\delta^{13}C$ signatures were observed in the green *Ulva intestinalis* (*Enteromorpha intestinalis*), with values ranging from −8.81‰ to −20.30‰ (Maberly et al. 1992), and the browns *Adenocystis utricularis* (−8.81‰ to −20.30‰, Dunton 2001; Raven et al. 2002b) and *Colpomenia peregrina* (−6.14‰ to −12.09‰, Raven et al. 1995, 2002b).

19.4 Calcification

The biogenic formation of calcium carbonate from Ca^{2+} and CO_3^{2-} is termed calcification. Three polymorphs of calcium carbonate are made by seaweeds: calcite, aragonite, and high-magnesium calcite, and in the present-day surface ocean, these are supersaturated so that biogenic precipitation by algae is "thermodynamically favored" (Raven and Giordano 2009). However, the lower pH predicted for future oceans causes a reduction in the saturation state of the carbonate ion, making it more difficult for calcifying organisms to calcify (Cao and Caldeira 2008). High-magnesium calcite, synthesized by coralline seaweeds, is the most soluble polymorph, potentially making this group most susceptible to OA. The site of calcification varies among seaweeds. For example, coralline seaweeds deposit high magnesium calcite into their cell walls, the brown genus *Padina* deposits a fine layer of aragonite onto its cell surface, and for the tropical genus *Halimeda*, aragonite mineralizes in the intercellular spaces between the utricles (Stanley 2008; Raven and Giordano 2009; Nelson 2009; Ries 2009, 2010).

There have been few studies (e.g., Borowitzka and Larkum 1976; Borowitzka 1987) on the underlying physiological mechanisms of calcification in seaweeds, but the recent interest in OA has stimulated research in this important area (see Ries 2009, 2010). Photosynthesis (and primary production) and calcification are thought to be intimately linked because rates of calcification are enhanced in the light, but the mechanisms are not fully understood (Ries 2009, 2010). Also affecting calcification rate is the ratio of magnesium to calcite (Mg/Ca ratio) and the carbonate saturation state, both of which are influenced by pH (Ries 2009, 2010). Over geological timescales, the world's ocean has switched between "aragonite seas" (today's ocean) and "calcite seas". When the green seaweeds *Halimeda*, *Penicillus*, and *Udotea* were grown in seawater with a Mg/Ca ratio > 2 (aragonite sea), rates of growth, calcification, and primary production were greater than when grown in

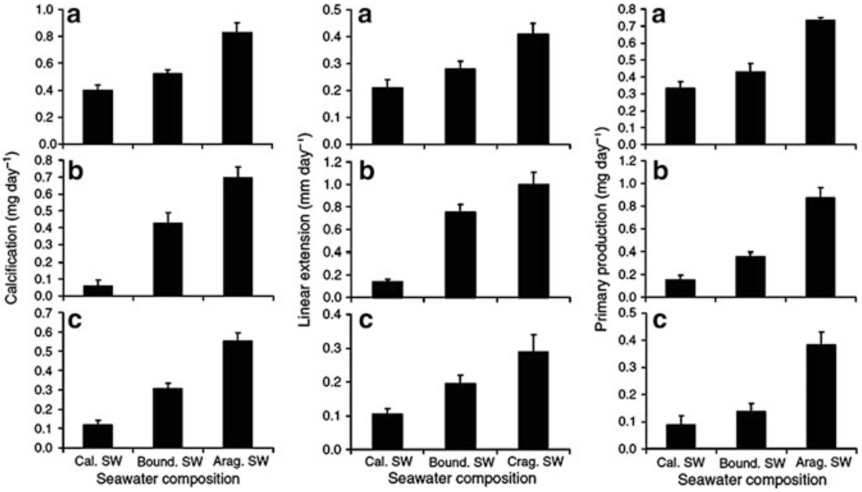

Fig. 19.2 Calcification, linear extension, and primary production in (**a**) *Halimeda*, (**b**) *Penicillus*, and (**c**) *Udotea* grown in experimental calcite, boundary, and aragonite seawaters. Rates of calcification, linear extension, and production significantly increase ($P < 0.05$) with increasing seawater Mg/Ca. *Vertical bars* are standard errors (From Ries 2009, with permission of Blackwell Publishing Ltd)

calcite seas (Fig. 19.2). In the calcite sea treatments, however, they were still able to precipitate aragonite, demonstrating some level of internal control over the polymorph of calcite produced. For coccolithophores (calcifying phytoplankton), the physiological basis of calcification, and its relationship to photosynthesis, is being elucidated using various physiological and molecular tools (e.g., Brownlee and Taylor 2004); similar approaches need to be applied to calcifying red, green, and brown seaweeds if we are to better understand how they will be affected by OA.

19.5 Physiological Performance in a High CO_2 World

The sensitivity of seaweeds to OA can be species specific. Their response may vary depending on their carbon physiology, mode of calcification, morphology (functional growth forms), and life history. For example, filamentous turf algae with shorter generation times may be able to acclimate and adapt to the changing environment faster than large canopy-forming kelp species with a longer generation time.

19.5.1 Noncalcifying Seaweeds

CCM activity in algae is in most cases associated with the ability to use, indirectly or directly, HCO_3^- ions (e.g., Smith and Bidwell 1989; Björk et al. 1992, 1993; Axelsson et al. 1999, 2000; Mercado et al. 2006). Since the shift in DIC species due to increased atmospheric CO_2 will result in a small proportional change in HCO_3^- compared to CO_2 and CO_3^{2-} concentrations, this will confer no/little advantage on species relying on HCO_3^- use for carbon acquisition (Beardall et al. 1998). Consequently, species with an active CCM are unlikely to show stimulation of photosynthesis or growth with an increase in atmospheric CO_2 levels. Conversely, when modern day terrestrial C_3 plants were grown at Glacial CO_2 concentrations (180–200 ppm), they exhibited a reduction in photosynthesis and growth, and delayed reproduction (Ward 2005; Gerhart and Ward 2010). Further long-term studies on seaweed's response to high CO_2 of the future and low CO_2 of the past may provide crucial understanding on their adaptive capability to changing CO_2 over geological and evolutionary timescales.

Macroalgae grown at elevated CO_2 showed downregulation of CCM activity (e.g., *Fucus serratus*, Johnston and Raven 1991; *Ulva lactuca*, Magnusson et al. 1996) and the energy savings from downregulating CCM are hypothesized to increase growth, but no increase in growth rate was observed in brown seaweed species with known active CCMs, e.g., *Laminaria digitata* and *Saccharina latissima*, grown under Glacial, Preindustrial, and 750 ppm CO_2 concentrations (Roleda MY, Stecher A, Gutow L, Bartsch I and Wiencke C, unpublished data). Among red seaweeds, photosynthesis and growth rates of *Porphyra yezoensis* in culture were enhanced under high (1,000 and 1,600 ppm) CO_2 concentrations (Gao et al. 1991). Enhancement of growth with increasing CO_2 is also reported in *Gracilaria* species (Gao et al. 1993b). For the CO_2-user *Lomentaria articulata*, higher relative carbon growth (52%) was measured under 2× of the current ambient CO_2 compared to its growth (23%) under 5× CO_2 (Kübler et al. 1999).

At a high photon flux density (PFD), the seawater concentration of DIC becomes insufficient to saturate photosynthesis of intertidal algae (Mercado et al. 2001). Therefore, when photosynthetic rate exceeds the rate at which CO_2 is supplied, photosynthesis becomes inhibited (Murru and Sandgren 2004). Under such carbon-limiting conditions, employing the energetically expensive CCM becomes ecologically advantageous making most intertidal macroalgal species DIC saturated (e.g., Surif and Raven 1989, 1990, Beer 1994). Carbon acquisition in 38 species of red macroalgae showed that intertidal species used both dissolved CO_2 and HCO_3^- while subtidal algae are typically restricted to the use of DIC in the form of dissolved CO_2 (Murru and Sandgren 2004). Another study showed that three species of intertidal Gelidiales have a low affinity for HCO_3^- in their natural habitat (Mercado et al. 2001).

Because DIC availability is relatively high and replenished from carbonates in shells and rocks, DIC-limited aquatic photosynthesis is considered rare; however, there is evidence that some subtidal species are DIC limited, e.g., *Dilophus* *guineensis*, *Lobophora variegata*, and *Laurencia papillosa* collected at 3–5 m depths, and *Turbinaria turbinata* collected at 10 m (Holbrook et al. 1988). But if in situ photosynthetic rates of deep macroalgal species are light limited, they may essentially be DIC saturated under present-day CO_2 levels (Johnston et al. 1992, Surif and Raven 1989). Under elevated CO_2, downregulation of CCMs among sublittoral macroalgal species growing under light limited conditions will require less light energy for HCO_3^- transport; this energy saving may stimulate growth rate (Hepburn et al. 2011).

19.5.2 Calcifying Seaweeds

Calcified macroalgae, represented by members of phylogenetically diverse brown, green, and red species, are distributed from polar to tropical latitudes and inhabit shores ranging from the mid-high intertidal to the deepest reaches of the euphotic zone. These macroalgae produce marine sediments for reef accretion, provide three-dimensional habitat structure functioning as autogenic ecosystem engineers, contribute structural frameworks for coral reef ecosystems, and play critical ecological roles for invertebrate recruitment processes (reviewed by Nelson 2009, Ries 2009, 2010).

Regardless of the increased DIC availability, the severe consequences of the predicted lower pH and lower carbonate concentration to calcifying macroalgae are relatively well documented. The most studied calcified macroalgal group in relation to OA belongs to the red algal order Corallinales. Calcification in *Corallina pilulifera* is inhibited at pH 7.6 compared to 8.2 (Gao et al. 1993a). A 20% decrease in calcification was also observed in *Hydrolithon* sp. when incubated at 900 ppm CO_2 (pH = 7.8), while the photosynthetic rate was enhanced by 13% (Semesi et al. 2009b). For the green seaweed *Halimeda tuna* from the Great Barrier Reef, calcification declined when exposed to a pH of 7.5 compared to 8.0 (Borowitzka and Larkum 1986).

The fundamental changes in carbonate chemistry of seawater due to increasing atmospheric CO_2 levels may enhance the competitive advantage of noncalcifying over calcifying species (e.g., Fig. 19.5, Hall-Spencer et al. 2008; Kuffner et al. 2008). Moreover, its interaction with increasing sea surface temperatures may have serious impacts on calcifying macroalgae, associated biota, and coastal ecosystems as a whole.

19.6 Natural Fluctuations in Seawater Carbonate Chemistry

Most projections on how seawater carbonate chemistry and pH will change in the coming decades are based on the open ocean, where pH is relatively stable and only tends to vary on annual cycles. In coastal oceans, however, local-scale processes

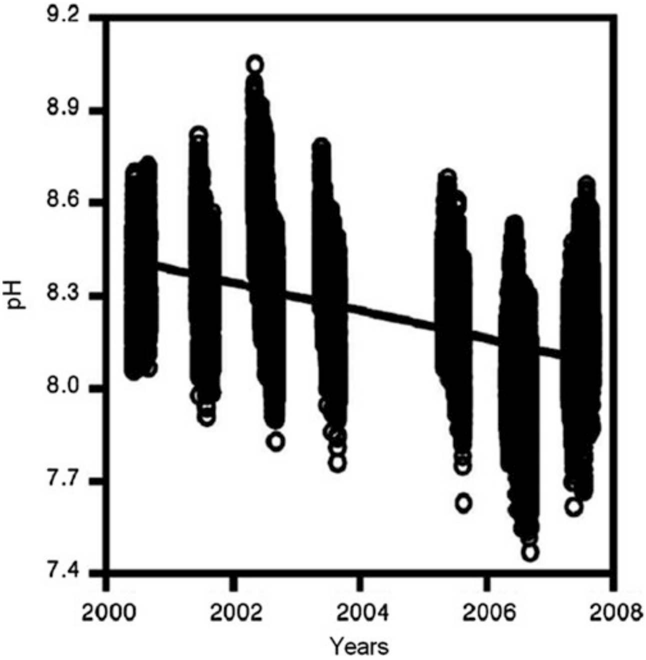

Fig. 19.3 Interannual variation in ocean pH at Tatoosh Island ($n = 24{,}519$). pH measurements as a function of date and time between 2000 and 2007, with significant decline ($P < 0.05$). (From Wootton et al. 2008, with permission of National Academy of Sciences)

including upwelling (Feely et al. 2010), river outflows (Mathis et al. 2011), and metabolic activity of the primary producers themselves (Semesi et al. 2009a) also alter pH. Predicting the effects of OA on coastal communities thus requires field information on the natural daily cycles of pH encountered by organisms in the field.

Coastal ocean pH measurements spanning 8 years around Tatoosh Island in the eastern Pacific revealed several patterns contrary to the historical perspective that ocean is well buffered (Wootton et al. 2008). A diurnal pH oscillation of 0.24 units is due to daily variation in photosynthesis (CO_2 uptake) which causes pH to increase during the light and decrease at night due to respiration and diffusion from the atmosphere which replenish CO_2 (Bensoussan and Gattuso 2007) causing a pH decline. A complex seasonal pattern in pH variation was also observed that is linked to key physical and biological drivers with known mechanistic ties to pH (cf Wootton et al. 2008). Looking at the entire temporal span of the data from year 2000 to 2008, however, a general trend of declining pH is apparent which can be attributed to the effect of increasing atmospheric CO_2 (Fig. 19.3; Wootton et al. 2008).

Diurnal variation in pH, total alkalinity (TA), and DIC within a seagrass bed is related to tidal fluctuations (Semesi et al. 2009a). During low tide, restricted water motion, higher irradiance, and temperature caused enhanced rates of seagrass photosynthesis which resulted in pH increasing from 7.9 to >8.9 and a decrease in TA and DIC. On the incoming tide, the pH was lowered and DIC and TA increased, effectively buffering the system. Such an upward shift in seawater pH due to photosynthesis also affects the physiology of local organisms. For example, higher pH (10.1), lower inorganic carbon (DIC = 0.6 mM), and possibly a supersaturated O_2 condition generated by *Ulva intestinalis* in temperate rockpools inhibit the growth of *Fucus vesiculosus* and *Chondrus crispus*; these species normally coexist in the eulittoral where the prevailing natural open water chemistry lies at pH 8.2 and 2.2 mM DIC (Björk et al. 2004). Conversely, biologically induced increases in pH (>1 pH unit) in a tropical seagrass meadow caused higher calcification rates of three seaweeds species in the community, *Hydrolithon* sp. and *Mesophyllum* sp., and *Halimeda renschii* (Semesi et al. 2009a).

Spatial and seasonal variations in $p\text{CO}_2$ and DIC are also observed in sub-Antarctic kelp beds (Delille et al. 2000, 2009). Outside the kelp bed, the buffer factor (β) indicates that DIC dynamics are mainly influenced by air–sea exchange and photosynthesis, but inside the kelp bed, β suggests that DIC dynamics are controlled by calcification by the epiphytic community (Delille et al. 2000). Diel variations in $p\text{CO}_2$ and DIC were prominent in spring and summer but absent in winter. The seasonal drivers responsible for variations in $p\text{CO}_2$ and DIC are the higher photosynthetic rates in spring and summer, and the decay of organic matter in autumn which leads to a strong oversaturation of $p\text{CO}_2$ (Delille et al. 2009).

The above examples illustrate that seaweeds themselves modify the carbonate chemistry of the surrounding seawater (in terms of total alkalinity, $p\text{CO}_2$, DIC, and pH) due to their metabolic activities. This ability of seaweeds to modify their local environment needs to be taken into account in future experiments to test the effects of OA on individual seaweeds and communities.

19.7 Physicochemical Coupling

19.7.1 Water Motion and Diffusion Boundary Layers

At the surface of all aquatic organisms that have metabolic exchange across their outer surface (i.e., plankton, seaweed, and some invertebrates) is a diffusion boundary layer (DBL), a region of stagnant water across which molecules and ions move by molecular diffusion (Hurd et al. 2011). In seaweeds, the thickness of the DBL depends on thallus morphology, seawater velocity, and the type of water motion (waves vs. currents) (Hurd 2000; Hurd and Pilditch 2011). The traditional view is that thick DBLs reduce seaweed growth rates because the flux of essential nutrients (including inorganic carbon) is hampered, but there is little empirical data to support this for temperate seaweeds (reviewed by Hurd and Pilditch 2011). Metabolic processes at the seaweed surface cause the local pH to increase (photosynthesis) and decrease (respiration and calcification). Laboratory experiments demonstrate that under slow flows that are typical of many subtidal habitats (<5 cm s^{-1}), the pH at the surface of the seaweed could be considerably higher

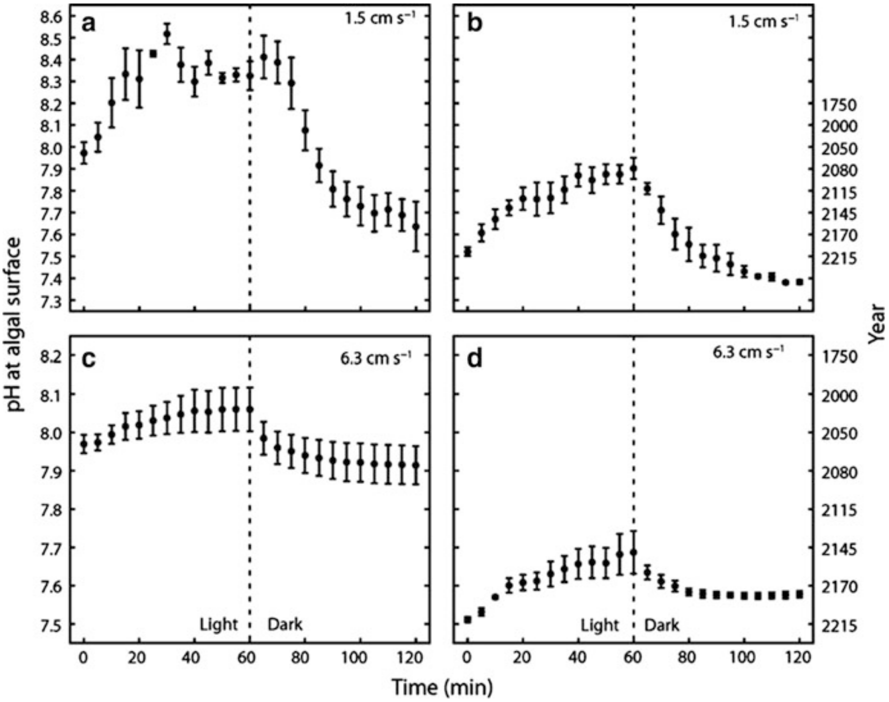

Fig. 19.4 pH fluctuations at the surface of the coralline seaweed *Sporolithon durum* measured for 1 h in the light and 1 h in the dark at an initial seawater pH of ~7.9 (**a**, **c**) and ~7.5 (**b**, **d**) at mainstream velocities of 1.5 cm s^{-1} (**a**, **b**) and 6.3 cm s^{-1} (**c**, **d**). Data are also plotted against modeled pH of surface waters (right-hand side) projected on centennial timescales, i.e., for the period 1750–2215 (Caldeira and Wickett 2003). *Symbols* represent the mean of three replicates (±1 s.e.m.). (Modified from Hurd et al. 2011, with permission of Blackwell Publishing Ltd)

or lower than that of the bulk/mainstream seawater (De Beer and Larkum 2001; Hurd et al. 2011). For example, in the light, at a mainstream flow of 1.5 cm s^{-1}, pH at the surface of *Sporolithon durum* increases to ~8.4 and declines to ~7.65 in the dark (Fig. 19.4a, Hurd et al. 2011). As seawater velocity increases, the range of these surface pH fluctuations declines because the DBL is thinner (Fig. 19.4c). When the mainstream seawater pH is decreased to 7.5 (worst-case scenario for 2215), *S. durum* is still able to raise the surface pH by 0.2 units in the light at flows of 6.3 cm s^{-1} (Fig. 19.4d) illustrating an ability to biologically modify the local pH environment, at least in the short term.

The ubiquitous nature of DBLs has implications for how seaweed communities might respond to OA. Seaweeds growing on wave-impacted shores or in fast flowing currents will experience a pH at their surface that will be similar to that of the mainstream seawater because DBLs will be thin: there are exceptions to this, however, because some seaweeds such as the giant kelp *Macrocystis pyrifera* have small (<1 mm) morphological features that trap seawater and cause thick DBLs (0.67 mm) even under fast flows. Similarly, at flows of 1.5 cm s^{-1}, the coralline red

Sporolithon durum has DBLs that are up to 1.7 mm thick, and although DBL thickness declines as seawater velocity increases, average DBL thickness at a mainstream velocity of 10 cm s^{-1} ranges from ~0.2 to 0.4 mm. In wave-sheltered sites, or for small, foliose or turf-forming algae in understory canopies, the seawater velocity at the seaweed surface will be much slower than that of mainstream flows, and they may encounter a wide range of pHs at their surface; this range is likely to vary on daily and tidal cycles. Therefore, the possibility exists that at their surface, many seaweeds naturally experience pH at night that are as low as those predicted for OA, and during the day pH at their surface, will increase, perhaps ameliorating any detrimental low-pH effects. Essentially, seaweeds in slow flows may be adapted to a wider range of pH fluctuations than those in fast flows which has implications for differential susceptibility of organisms to OA (Hurd et al. 2011). However, experiments examining the effects of water motion on the susceptibility to OA have been over short timescales (hours) and the question is whether over the long term (i.e., generations) seaweeds will have the physiological flexibility to adapt to lower pH seawater.

19.7.2 Temperature and Regional Vulnerability

Due to the greater CO_2 solubility in cold waters, seawater is expected to acidify more strongly making high latitude and polar regions more vulnerable to OA compared to tropical regions (McNeil and Matear 2008). Likewise, carbonate ion concentrations are highest in the tropics and decrease poleward in concert with decreasing temperature (see also Chap. 18 by Bartsch et al.). Carbonate ion concentrations will therefore remain higher in warmer parts of the oceans, so calcification rates in these regions should remain higher than in cooler regions. However, tropical coral reef ecosystems will be affected in multiple ways by rising CO_2, but most directly by the simultaneous changes in temperature and in seawater chemistry. Differential responses among populations of cosmopolitan species, or species with broad latitudinal distribution, to OA and greenhouse conditions (high CO_2 and high temperature) will be an important line of investigation. For example, comparisons could be made between tropical, temperate, and arctic populations of cosmopolitan macroalgae (e.g., *Acrosiphonia, Ulva, Plocamium*), and different *Macrocystis* populations; this species is widely distributed throughout the continental margins of the northern (Alaska to Mexico) and southern (Peru to southernmost Chile) Pacific Ocean, and is also found in isolated regions of South Africa and around most of the sub-Antarctic islands to 60°S (Graham et al. 2007). A poleward shift in the geographic range of major subtidal kelp species has been suggested for future climate scenarios in marine coastal ecosystems (Merzouk and Johnson 2011).

19.7.3 pH, Chemical Speciation, and Nutrient Availability

The effect of OA on seawater chemistry goes beyond the carbonate system (see also Chap. 4 by Gordillo). Chemical species that may undergo speciation under lower pH include major (phosphorus, silicon, and nitrogen) and minor (boron) elements as well as trace elements such as iron and zinc (Doney et al. 2009). Moreover, the concentration of chemical species such as phosphate, silicate, and ammonia decreases with decreasing pH (Fig. 1.2.11 in Zeebe and Wolf-Gladrow 2001). Recently, a decline in oceanic nitrification rates is reported as a consequence of OA (Beman et al. 2011). The estimated 3–44% reduction in the next decades can affect oceanic nitrous oxide production, reducing oxidized nitrogen (NO_2^-, NO_3^-) supplies in the upper layers of the ocean, and fundamentally altering nitrogen cycling in the ocean (Beman et al. 2011). The consequence of nutrient speciation and their bioavailability to macroalgae is largely unknown; fractional changes may alter photosynthesis, growth, and nutritional value which could affect the rest of the food web (see Sect. 19.8.1). Likewise, dissolved organic matter (DOM) which undergoes hydrolytic reactions in seawater, e.g., organic acids, amino acids, nucleic acids, proteins, and humic materials, will also be effectively altered by changing pH (Doney et al. 2009). Therefore, the overall impact of decreasing pH on these biologically important organic compounds requires further in-depth investigation.

19.8 Trophic Dynamics and Coastal Ecosystem Response

19.8.1 Stoichiometric Ratio of Aquatic Ecosystems

Interactions between global climate stressors (e.g., CO_2 and temperature) and local perturbation (e.g., eutrophication) will not only cause regime shifts in coastal ecosystems favoring spatial expansion of ephemeral turfs and persistence beyond their normal seasonal limits (Russell and Connell 2009) but also stoichiometry of aquatic ecosystems.

When the ocean becomes enriched with carbon due to rising levels of atmospheric CO_2, the associated warming and vertical stratification of water suppresses nutrient supply from deep water into the surface layers. The consequent increase in carbon and decrease in nutrient concentration results in an increase in the cellular carbon:nutrient ratio. Phytoplankton with high carbon-to-nutrient ratios are of low nutritional value for zooplankton; such change in stoichiometry may cascade throughout the entire aquatic food web (van de Waal et al. 2010).

Conversely, if a coastal ecosystem receives a concurrent high supply of nutrients of anthropogenic sources, the probable consequence of altering the carbon:nutrient ratios of seaweeds, and their nutritional values to herbivorous fishes and invertebrates, is largely underappreciated. For example, the molar C:N ratio of *Ulva rigida* under nitrogen-limited conditions increased by ~10% when the CO_2 concentration was increased from 350 to 10,000 ppm. However, when the elevated CO_2 condition was coupled with a 20× increase in nitrogen, a >20% decrease in C:N ratio was observed (Gordillo et al. 2001). On the other hand, significant increases in the C:N ratio in a marine angiosperm, *Thalassia hemprichii*, is reported under increasing CO_2; the increase in tissue carbon content was seen as a positive

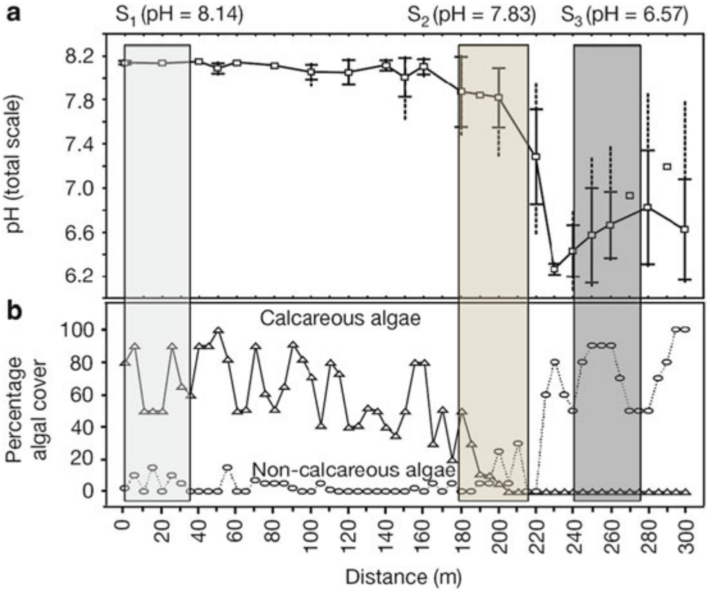

Fig. 19.5 Variation in pH at CO_2 vents south of Castello d' Aragonese (Ischia Island, Italy) and abundance of macroalgae. (**a**) Mean pH ± s.d. data from stations S1–S3. (**b**) Percent cover of calcareous (*triangles*) and noncalcareous macroalgae (*circle*). (Modified from Hall-Spencer et al. 2008, with permission of Macmillan Publishers Limited)

response to OA in coastal seas (Jiang et al. 2010). However, neither study considered the consequence of the shift in C:N ratio on ecosystem trophic dynamics.

19.8.2 Community Structure

Natural volcanic CO_2 vents have conditions comparable to the high CO_2/low pH conditions progressively developing in oceans through the uptake of fossil-fuel CO_2. Hall-Spencer et al. (2008) used this natural ecosystem to demonstrate the effect of OA on biodiversity and ecosystem structure and function. They showed that organisms such as sea urchins, coralline algae, and stony corals decline in abundance or completely disappear with decreasing pH close to the vents, while seagrasses and brown algae benefit from elevated CO_2 availability close to the vent by increasing their biomass. Percentage cover of calcareous algae dropped from >60% outside the vent area (S1, pH = 8.14) to zero cover within it (S2–S3, pH = 7.83–6.57), while the reverse was observed with noncalcareous algal cover (Fig. 19.5). Macroalgae observed to be resilient to naturally high amounts of pCO_2 include *Caulerpa*, *Cladophora*, *Asparagopsis*, *Dictyota,* and *Sargassum.* This study showed that lowered pH due to OA, even without global warming that is associated with rise in atmospheric CO_2, can bring about loss in biodiversity and shift in ecosystem structure and function (Hall-Spencer et al. 2008). Recently, Porzio et al. (2011) showed that reproduction of some resilient seaweeds was not affected under extremely high CO_2 conditions near the volcanic CO_2 vents.

Manipulative experiments (using the HCl method of pH manipulation) showed that OA, at 2× present day (pH = 7.91), is responsible for a 79% reduction in crustose coralline algae (CCA) recruitment, 40% reduction in growth rate and 92% reduction in cover, and a 52% increase of a mixed assemblage of noncalcifying algae composed of macroalgal germlings, diatoms, and small filamentous algae (Kuffner et al. 2008). Likewise, using multispecies Markov chain models, a method used to link environmental change to species dynamics, Wootton et al. (2008) showed a strong link between in situ benthic species dynamics and variation in ocean pH. They showed that the abundance of calcareous invertebrate species generally declined with declining pH while fleshy algae (*Halosaccion glandiforme*, ephemeral algae, filamentous red algae, and foliose red algae) increased with declining pH.

Elevated CO_2 may potentially influence competitive exclusion of certain species within a community. Quantification of carbon uptake mechanism (using carbon isotope and pH drift methods) within a kelp forest community showed that the canopy (Laminarians and Fucaleans) and dominant understory species (calcifying coralline algae) all had functional CCMs, while the less dominant understory species, consisting of mostly red noncalcifying species, relied on diffusive CO_2 uptake and had no functional CCMs (Hepburn et al. 2011). Results of the above study suggest that in the low-pH coastal waters of the future, the growth rates and competitive abilities of noncalcifying and CO_2-only seaweeds will increase, while those of calcifying CCM seaweeds will decrease. This could cause major shifts in community structure, altering functional diversity and near shore ecosystem functioning (Hepburn et al. 2011). However, it is difficult to predict how ecosystems might change because some HCO_3^--using species can switch to CO_2 use at lower pH 7.5, thereby increasing the energy available for growth and reproduction (Cornwall et al. 2012).

19.8.3 Interactive Effects of Ocean Acidification and Other Stressors

The results of single-factor experiments may be different, or the physiological response be of a lower magnitude, compared to the interactive effects of multiple stressors that most seaweeds are exposed to in their natural habitats. For example, calcification rate of CCA *Lithophyllum cabiochae* was not affected when independently exposed to elevated CO_2 or temperature. However, when exposed to a combination of elevated CO_2 and temperature, calcification rates decreased by 50% and an accelerated and extensive (~60%) tissue necrosis was observed (Martin and Gattuso 2009). Higher sensitivity to OA under higher temperature is also reported in the CCA *Hydrolithon onkodes* which sustained higher skeletal dissolution and concurrent increase in the abundance of their co-habiting endolithic algae (Diaz-Pulido et al. 2012).

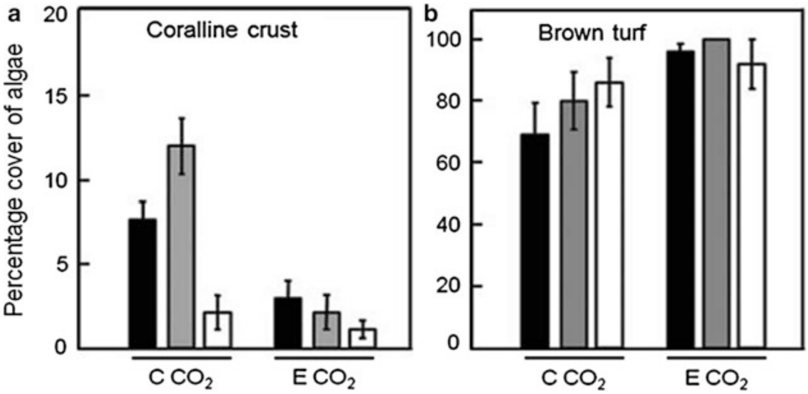

Fig. 19.6 Percentage cover (mean ± SE) of (**a**) coralline crusts and (**b**) turfs recruited to unoccupied substrates when exposed to crossed combination of CO_2 (control [CCO_2] vs. elevated [ECO_2]) and light (shade vs. low UV vs. full sunlight; in *black, gray, and white bars*, respectively). (From Russell et al. 2011, with permission of Blackwell Publishing Ltd)

On the other hand, elevated CO_2 concentration (1,000 ppm) in synergy with ultraviolet radiation is reported to systemically negatively impact the physiology of an articulate coralline alga *Corallina sessilis* in terms of photosynthesis, photosynthetic and accessory pigments, growth, and calcification rates (Gao and Zheng 2010). Positive effects of elevated CO_2 in synergy with other environmental stressors are also reported. Emersed net photosynthesis of *Porphyra haitanensis* increased with higher CO_2 (700 ppm), temperature, and level of desiccation (Zou and Gao 2002).

At the community level, the synergistic effect of global increase in CO_2 and a local stressor such as eutrophication can select for resilient species and cause phase shifts in coastal ecosystem. For example, the combined effect of high CO_2 and nutrients accelerates the expansion of filamentous turfs at the expense of calcifying algae (Russell et al. 2009). Likewise, the synergistic effect of high CO_2 and high temperature favors the filamentous turfs over the kelps (Connell and Russell 2010). Conversely, increased photosynthesis and growth of seagrasses under nutrient replete and elevated CO_2 may benefit some calcifiers, as shown in the higher calcification rate of *Hydrolithon* sp. in the proximity of seagrasses, due to the drawdown of CO_2 from the water column (Semesi et al. 2009a).

Light (including ultraviolet radiation) is known for its role in shaping the subtidal ecology of photosynthetic organism (Bischof et al. 2006). However, Russell et al. (2011) found that the forecasted increase in CO_2 levels can alter how light influences community structure. For example, under control CO_2 (pH = 8.06–8.16) the effects of light on the percent cover of the two groups of algae studied, the calcifying red crustose *Lithophyllum* sp. and the turf-forming brown *Feldmannia* spp., corresponded to their growth habitat's light environments: the subcanopy red coralline grew better under low UV while the highest cover of the brown turf was observed under full sunlight (Fig. 19.6). However, under elevated CO_2 (pH = 7.84–8.12), the influence of light on the percentage cover of understory crusts was substantially reduced (Fig. 19.6a) which caused crusts to grow less under all light treatments. Conversely, elevated CO_2 had the opposite effect of positively influencing turf cover (Fig. 19.6b), thereby reducing the structuring effects of light and UVB. Hence, to predict the ecological consequences of future CO_2 conditions, the role of contemporary processes (e.g., light and UVB) cannot be assumed to produce similar effects relative to other processes, which will change with a changing climate (Russell et al. 2011). Therefore, more studies are needed on the synergistic effects of different stress factors at the organism and community levels to better understand the biological and ecosystem impacts of OA.

19.9 Experimental Considerations

The possible effects of OA have been studied for ~10 years and an enormous volume of research has been produced during this time. Most studies have focused on reducing pH and measuring response variables of individual algae or communities. There are three methods available to lower SW pH: 1. addition of HCl, 2. bubbling with CO_2 gas, or 3. HCl/NaOH additions (Hurd et al. 2009; Riebesell et al. 2010). Methods 2 and 3 alter seawater carbonate chemistry in a way that mimics OA (TA remains constant, DIC increases), while using HCl, alkalinity decreases but there is no change in DIC. Importantly, two seawater carbonate parameters must be measured during experiments so that the carbonate speciation within experiments can be followed. Some first-generation OA experiments on seaweeds suffered from pseudoreplication or lack of independent replication (Hurd et al. 2009). However, with the design of new systems for controlling and monitoring pH, many of these experimental problems have been resolved (e.g., McGraw et al. 2010). Because seawater carbonate chemistry is complex, and because algae themselves modify their local pH environment, it is important that biologists and carbonate chemists collaborate on OA studies to avoid the many pitfalls that will result in a nonrigorous experimental design.

19.10 Conclusions and Future Works

The responses of ecosystems to OA are difficult to predict because all algae, calcifying and noncalcifying, could be affected. Most macroalgae are HCO_3^- users, and the predicted increases in DIC may have little effect on growth rates compared to seagrasses and seaweeds that rely on CO_2. For calcifiers, several studies have shown that calcification rates are depressed by increased levels of CO_2. This is one of the many indications of a negative biological response in the marine environment. Predicting the responses of ocean chemistry to rising CO_2 is reasonably straightforward (e.g., Caldeira and Wickett 2003), but with fairly modest biological data available, we cannot easily predict long-term species and community responses to climate and other environmental changes, and their feedback on climate in the future. Our present understanding of the potential effects of OA on marine organisms stems largely from short-term laboratory and mesocosm experiments. But chronic exposure to increased $p\mathrm{CO}_2$ may have complex effects that are different to, and/or not observed, in short-term experiments. For example, under long-term exposure to elevated CO_2, certain organisms may employ a range of mechanisms for adaptation. Moreover, the response of individual organisms, populations, and communities to a more realistic gradual increase in CO_2 is largely unknown (cf Boyd et al. 2008). Nevertheless, highly controlled short-term single or multifactorial laboratory experiments are also important in identifying the species' preadapted sensitivities to increasing CO_2. Considering that the CO_2 level expected in 2100 will be the highest for at least the past 24 million years, physiological acclimation and genetic adaptation might, at least in part, counteract adverse effects. Therefore, studies at molecular and genetic levels can contribute to understanding the genetic bases of resistance or resilience in marine macrophytes to changes in atmospheric CO_2 concentration.

The susceptibility of the early life history stages (reproductive cells, e.g., spores and gametes) as well as reproductive success (e.g., sporogenesis and gametogenesis) in the complex life histories of different seaweeds, e.g., bi- to triphasic, and heteromorphic involving microstages, under elevated CO_2/low pH needs to be addressed (e.g., Roleda et al. 2012). The microstages and juveniles are known to be more susceptible to environmental stressors compared to adult macrostages, e.g., life-stage-dependent UVR susceptibility (Roleda et al. 2007, 2009). Survival of the early life history stages to global climate change related stressors is essential for recruitment success to maintain species diversity and standing stock to sustain community metabolism.

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

Kai Bischof and Franciska S. Steinhoff

20.1 Introduction

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

20.4 Interaction with Other Abiotic Factors

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

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

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

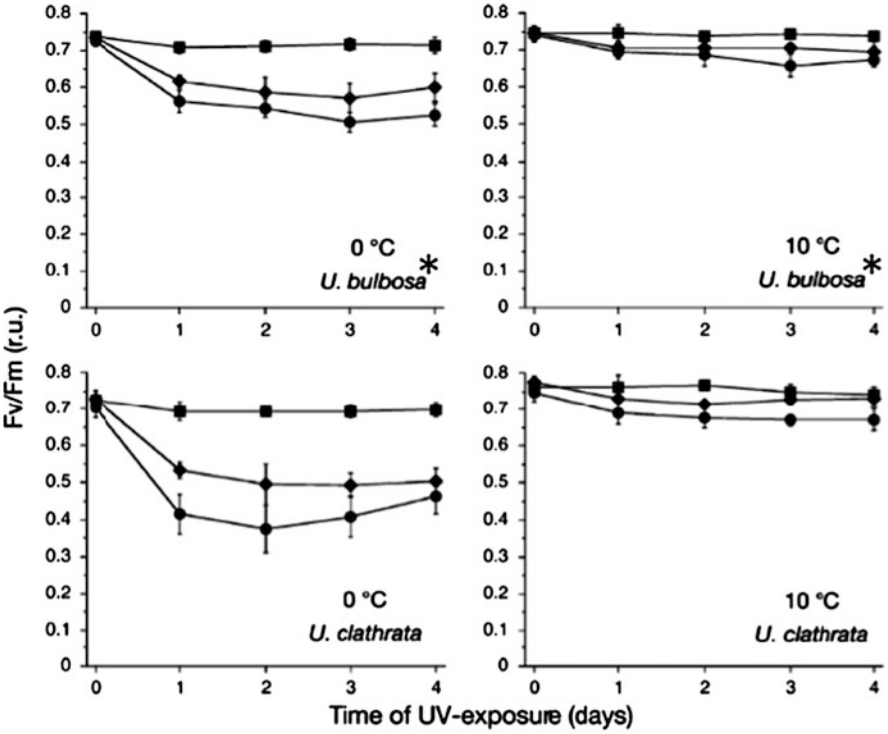

Fig. 20.1 Interactive effects of UV exposure and temperature on optimum quantum yield of photosynthesis (F_v/F_m): *Ulva bulbosa,* (*now also referred to as *U. hookeriana*) (isolated from King George Island, Antarctica) and *U. clathrata* (isolated from Puerto Williams, Tierra del Fuego, South America)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

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

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

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

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

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

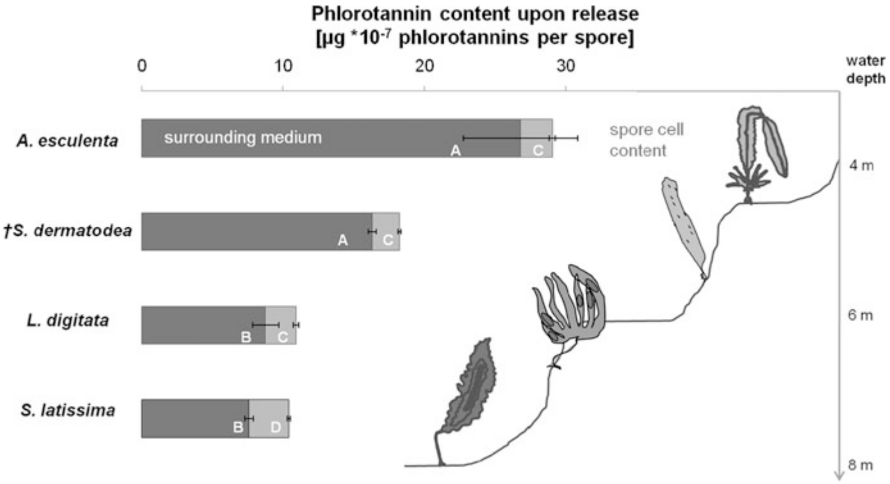

Fig. 20.2 Collection depth of *Alaria esculenta, Saccorhiza dermatodea* [†data from Steinhoff et al. (2011b)], *Laminaria digitata,* and *Saccharina latissima* from Kongsfjorden, Spitsbergen in correlation with the sum of phlorotannin content [µg × 10^{-7} phlorotannin spore^{-1}] within the surrounding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

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

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

20.5.1 Synthesis

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

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Chapter 21
Bottom-Up Versus Top-Down Control of Macroalgal Blooms

Mirta Teichberg, Paulina Martinetto, and Sophia E. Fox

21.1 Introduction

Macroalgal blooms are increasing worldwide and have many detrimental effects on ecosystems, including more frequent occurrences of anoxia, and loss of seagrasses, coral cover, and ecologically and commercially important species. The increased occurrences of macroalgal blooms have been attributed primarily to increases in the supply of the limiting nutrients, referred to as “bottom-up” control, and decreased grazer abundance due to overfishing and habitat degradation, referred to as “top-down” control. This chapter begins with an overview of the occurrence of macroalgal blooms worldwide and their ecological consequences. It discusses the role of coastal eutrophication and overfishing as the two main global drivers of bloom formations. The relative role of bottom-up versus top-down control in structuring ecological communities is controversial and has been heavily debated within the scientific community. This chapter will provide an overview of the main arguments of this debate in marine coastal waters. Specifically, scientific evidence supporting bottom-up versus top-down controls in shallow estuaries and coastal bays, coral reefs, and intertidal or subtidal rocky shores will be reviewed to understand how systems differ in response to these controls. We will provide an outlook on the future

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trends of eutrophication and overfishing and their impact on algal blooms in combination with other global changes. We will conclude with a discussion on management options to help reduce the escalation of bloom occurrences worldwide.

21.2 Occurrence of Macroalgal Blooms and Their Ecological Consequences

Macroalgal blooms are widespread along the coasts of the world (Table 21.1; Morand and Merceron 2005; Ye et al. 2011), forming dense mats or canopies in shallow estuaries and coastal lagoons (Valiela et al. 1992; Sfriso et al. 1992), accumulating on beaches as wrack (Morand and Merceron 2005), overgrowing corals (Smith 1981; Hughes 1994; Lapointe et al. 2005a, b), and affecting seagrass, soft-bottom, and rocky shore benthic communities (Díaz et al. 2002; Fox et al. 2009). Blooms of green, red, and brown macroalgae are common, although among these there are a few cosmopolitan species belonging to the genera *Ulva, Chaetomorpha, Cladophora*, *Gracilaria*, and *Pylaiella* (Table 21.1). Recent reviews on green algal tides showed bloom occurrences in most marine water bodies adjacent to highly urbanized or agricultural areas throughout Europe, Australia, New Zealand, Asia, and North and Central America (Morand and Merceron 2005; Teichberg et al. 2010; Ye et al. 2011). Some of the most famous examples of macroalgal blooms include the drift mats of *Ulva* spp. in Brittany, France (Morand and Merceron 2005) and Venice Lagoon (Sfriso et al. 1992; Sfriso and Marcomini 1997), *Cladophora* spp. in Peel Harvey Estuary, Australia (Lavery et al. 1991), and the more recent widely publicized *Ulva prolifera* blooms in the Yellow Sea, China during the 2008 summer Olympics with an estimated biomass of approximately 20 million wet tons (Liu et al. 2009; Gao et al. 2010; Ye et al. 2011).

Blooms of macroalgae have become a major ecological and economic problem in coastal habitats (Table 21.1, Fig. 21.1). Seaweed wrack accumulating on beaches can produce foul odors and release toxic hydrogen sulfide gas (Wilce et al. 1982), mats and deep canopies of seaweeds physically obliterate other primary producers including seagrasses (Valiela et al. 1997; Hauxwell et al. 2001; McGlathery 2001) and corals (Hughes 1994; Lapointe 1997; Lapointe et al. 2005a, b), and their decay causes anoxic conditions that lead to fish and shellfish kills (D'Avanzo et al. 1996; Valiela et al. 1997; Diaz 2001). Macroalgal blooms not only affect natural coastal communities and ecosystem function (Duarte 1995), but have high economic consequences by making coastal environments increasingly undesirable for recreational uses and threatening commercially important harvests (Valiela et al. 1992; Raffaelli et al. 1998; Oesterling and Pihl 2001). Often, the macroalgal species that form blooms are nonnative, such as *Gracilaria vermiculophylla*, *Codium* spp., and *Undaria pinnatifida,* and have the ability to quickly adapt to new environments and outcompete native species due to high stress tolerances, rapid nutrient uptake and growth rates, and varying reproductive strategies (Smith et al. 2002; Piriz et al. 2003;

Table 21.1 Examples of macroalgal blooms reported in different parts of the world's coastlines and some of their ecological and economic consequences (adapted from Teichberg et al. 2010)

Site	Seaweed taxa	Some effects	References
North America			
Gulf of California, Mexico	*Ulva, Gracilaria, Cladophora*	Anoxia, loss of species diversity	Ochoa-Izaguirre et al. (2002), Piñon-Gimate et al. (2008)
Nahant Bay, USA	*Pilayella*	Noxious odor, accumulated on beaches, nuisance to swimming and fishing	Wilce et al. (1982), Pregnall and Miller (1988)
Waquoit Bay, USA	*Cladophora, Gracilaria, Ulva*	Replaced seagrasses, anoxia, shell- and fin-fish kills	Valiela et al. (1997), Hauxwell et al. (2001), Fox et al. (2008)
Hog Island Bay, USA	*Ulva, Gracilaria, Codium*	Loss of species diversity	Thomsen et al. (2006)
San Francisco Bay, USA	*Ulva*	Anoxia, replaced benthic fauna	Fong et al. (1996)
Kaneohe Bay, Hawaii	*Dictyosphaeria*	Replaced corals	Smith (1981)
Southeast Florida, USA	*Codium*	Impact coral reefs	Lapointe et al. (2005a, b)
Bermuda	*Cladophora, Laurencia, Codium*	Anoxia, reduced benthic diversity and commercial fisheries	Lapointe and O'Connell (1989)
Southern California lagoons, USA	*Ulva*	Shifts in primary producers, anoxic conditions, cascading effects up food web	Kamer et al. (2001), Fong and Kennison (2010)
Europe			
Laholm Bay, Sweden NW Baltic Sea	*Ulva, Cladophora*	Replaced seagrasses, nuisance to swimming fishing and boating	Baden et al. (1990), Rosenberg et al. (1990)
Maasholm Bay, Germany	*Ulva, Pilayella*	Replaced native macroalgae, lowered benthic diversity and fishery yield, nuisance to swimming, fishing, and boating	Lotze et al. (2000), Worm et al. (1999)
Mondego Estuary, Portugal	*Ulva*	Replaced seagrasses, reduced benthic diversity	Martins et al. (2001), Cardoso et al. (2004)
Venice Lagoon, Italy	*Ulva, Gracilaria, Dictyota,*	Anoxia, fish kills, nutrient re-release, phytoplankton blooms	Sfriso et al. (1992), Sfriso and Marcomini (1997)

(continued)

Table 21.1 (continued)

Site	Seaweed taxa	Some effects	References
South America			
Nuevo Gulf and San Antonio Bay, Patagonia, Argentina	*Ulva, Undaria*	Accumulated on beaches, interferes with recreational uses	Díaz et al. (2002), Piriz et al. (2003), Teichberg et al. (2010), Martinetto et al. (2011)
Asia			
Quingdao, China	*Ulva*	Loss of species diversity, accumulated on beaches and nuisance for recreational activities	Liu et al. (2007, 2009)
Seto Inland Sea, Japan	*Ulva*	Replaced seagrasses	Sugimoto et al. (2007)
Australia			
Peel-Harvey Estuary, Western Australia	*Cladophora, Ulva, Chaetomorpha*	Accumulated on beaches	Lavery et al. (1991)
Tuggerah Lakes Estuary, New South Wales	*Ulva*	Replaced seagrasses, reduced benthic diversity	Cummins et al. (2004)
Africa			
Saldanha Bay, South Africa	*Ulva*	Competed with other commercial use algae	Anderson et al. (1996), Monteiro et al. (1997)

Lapointe et al. 2005a; Thomsen et al. 2006). Invasive macroalgae have often become nuisance species causing major damage to coastal benthic communities, reducing marine biodiversity, and altering food webs (Schaffelke and Hewitt 2007, see Chap. 12 by Andreakis and Schaffelke).

21.3 Coastal Eutrophication

One of the main triggers of macroalgal blooms is increased nutrient loading due to rapid urbanization and development of the coastal zone (Howarth 2008). Coastal eutrophication can be described as the increase in organic matter, including extensive blooms of phytoplankton and ephemeral macroalgae, due to nutrient loading along the coast (Nixon 1995; Cloern 2001). Cloern (2001) provides a detailed review and conceptual model of the rapidly changing problem of coastal eutrophication. This conceptual model describes both direct and indirect responses to increased nutrient loading along the coast, including increases in phytoplankton and macroalgal biomass, and changes in biogeochemistry, water transparency, and

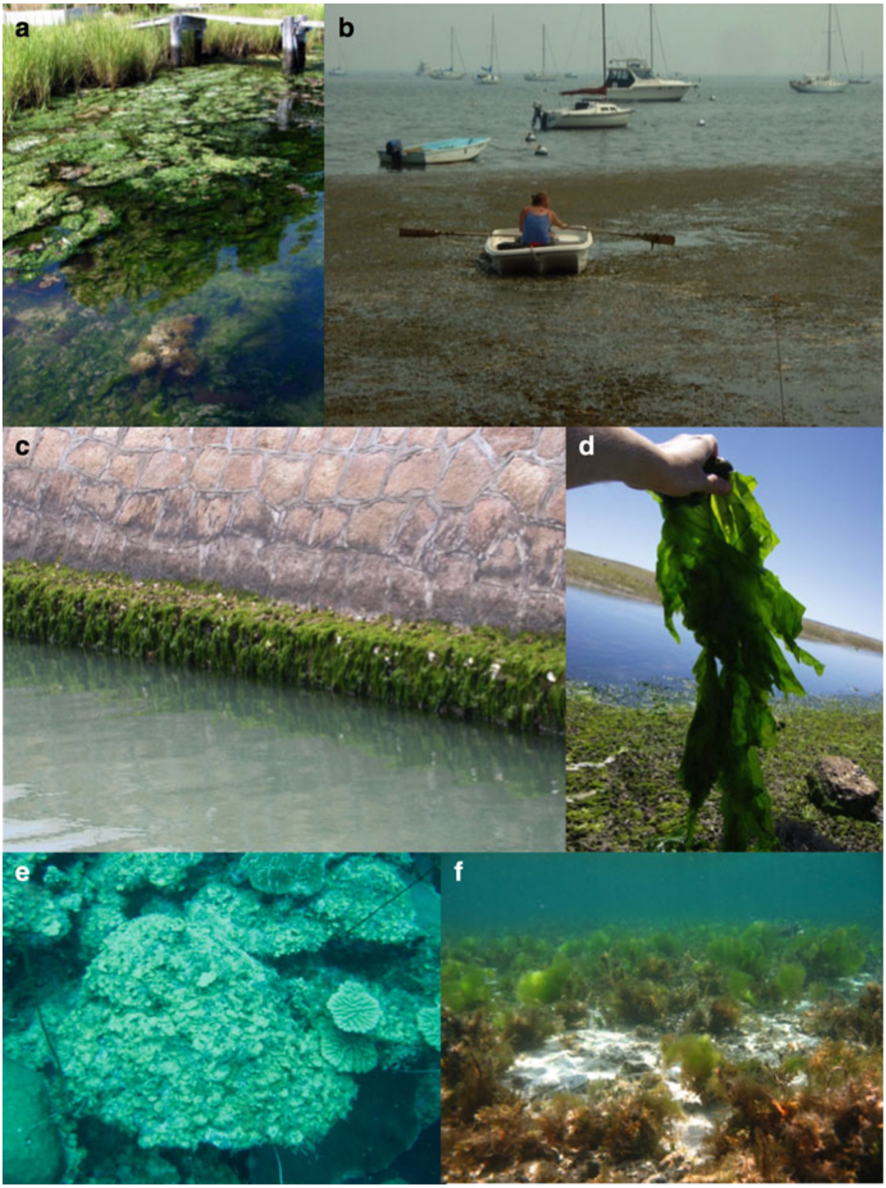

Fig. 21.1 Macroalgal blooms in estuaries and coral reefs habitats: (**a**) blooms of *Ulva lactuca* (photo by Ylva Olsen) and (**b**) *Cladophora variegata* (photo by Gabrielle Tomasky Holmes) along the subestuaries of Waquoit Bay, Cape Cod, USA; (**c**) *Ulva* spp. blooms attached to the walls in Venice Lagoon, Italy (photo by Mirta Teichberg) and (**d**) in the intertidal channel of San Antonio Bay, Argentina (photo by Paulina Martinetto); (**e**) *Lobophora variegata,* overgrowing coral reefs in Curaçao, Netherland Antilles (photo by Anna Fricke); (**f**) blooms of the green and brown macroalgae *Chaetomorpha* and *Dictoya* spp. on reef flats of Spermonde Archipelago, Indonesia (photo by Mirta Teichberg)

habitat quality. Most large occurrences of algal blooms have been associated with increased nutrient enrichment, primarily nitrogen, although phosphorus may also play a role (Howarth 2008; Teichberg et al. 2010). Here, we focus primarily on occurrences of macroalgal blooms reported worldwide that are linked to coastal eutrophication. Ecophysiological uptake and utilization mechanisms of nutrients, nitrogen and phosphorus limitation, assimilation of carbon, and the role of nutrient availability in stimulating macroalgal growth rates are reviewed in the Chap. 4 by Gordillo.

In the USA, approximately 65% of estuaries surveyed showed moderate to high levels of eutrophic conditions, influenced primarily by land-based nutrient loads from human activities (Bricker et al. 2008). In many of these estuaries, extensive chlorophyte and rhodophyte blooms are prevalent and have caused anoxic conditions (Bricker et al. 2008) and changes in the benthic community (Table 21.1). Waquoit Bay, in Cape Cod, Massachusetts, serves as a good example of how increased urbanization has led to drastic changes in the marine community structure over the past six decades (Valiela et al. 1992, 1997; Hauxwell et al. 1998, 2001; Fox et al. 2008). Macroalgal blooms of *Cladophora*, *Gracilaria*, and *Ulva* spp. have been directly linked to increased nitrogen loading rates in the subestuaries of Waquoit Bay predominantly due to increases in wastewater nitrate from septic systems that enters the estuary via groundwater (Valiela 2006; Fox et al. 2008; Fig. 21.1). Along the Florida coast, blooms of green macroalgae, including invasive species of *Codium* and *Caulerpa*, and drift red macroalgae have also been linked to increasing in nutrient inputs from sewage, shown through their high tissue N and P content and heavier nitrogen isotopic signatures that reflect that of wastewater nitrogen (Lapointe et al. 2005a, b; Lapointe and Bedford 2007, 2010).

Outside of North America, frequency of macroalgal blooms driven by high nutrient loads has also been reported (Table 21.1). Most sites where macroalgal blooms reach a remarkably high standing crop are locations where waters are enriched with nutrients as a result of urban growth in surrounding areas. A 20-year study in Peel Harvey Estuary, Australia, showed how large blooms of *Cladophora*, *Ulva*, and *Chaetomorpha* spp. have been caused by high nutrient loading, with interannual differences in biomass associated with nutrient and light conditions (Lavery et al. 1991). In San Antonio Bay, Argentina, high wastewater nitrogen and phosphorus inputs have been linked to high growth rates and biomass of *Ulva lactuca* that forms extensive blooms in the main channel of the bay (Teichberg et al. 2010; Martinetto et al. 2011; Fig. 21.1). Other sites known for macroalgal blooms that have been linked to coastal pollution include Venice Lagoon, Italy and Mondego Estuary, Portugal (Table 21.1, Fig. 21.1). In these sites, *Ulva* blooms persist under high nutrient loads (Sfriso et al. 1992; Martins et al. 2001; Teichberg et al. 2010).

21.4 Overfishing

Drastic changes in consumer abundance due to the overharvesting of commercially and recreationally important fish, mammal, and invertebrate species have occurred in many marine ecosystems throughout history (Jackson et al. 2001). A recent study shows approximately 90% of predatory fish stocks have been removed by fishing fleets worldwide (Myers and Worm 2003) with cascading effects down to lower trophic levels (Hughes 1994; Jackson et al. 2001; Mumby et al. 2006). Here, we focus on the role overfishing plays in the occurrence of macroalgal blooms in marine coastal waters. A classification of the different type of seaweed grazers and an overview of algal–herbivore interactions can be found in detail in Chap. 8 by Iken.

Most cases where overfishing has directly impacted macroalgal growth occur in coral reef and kelp ecosystems. This is due primarily to the number of relatively larger and ecologically important consumers that have been removed from these ecosystems compared to others (Jackson et al. 2001). Overharvesting of herbivorous fish, marine mammals, and invertebrates that directly graze on macroalgae have led to increased occurrence of macroalgal blooms in coral reefs (Hughes 1994; Jackson et al. 2001; Mumby et al. 2006). The opposite trend has occurred in kelp forests, where the removal of large consumers has often led to increases in invertebrate grazer abundance which then reduce macroalgal cover in these systems (Estes and Duggins 1995; Jackson et al. 2001).

It has been argued that shifts in benthic and pelagic communities due to overfishing long predated coastal eutrophication problems in marine systems (Jackson et al. 2001; Lotze and Milewski 2004; Heck and Valentine 2007). A review paper by Heck and Valentine (2007) stressed the importance of overfishing in regulating ecosystem structure by indirectly leading to altered food webs. They support that many of the negative effects on coastal ecosystems attributed to coastal eutrophication may actually be confounded by indirect effects of historical changes in consumer abundances. They state that most manipulative experiments that test the importance of nutrients and consumers on benthic ecosystems today are doing so in ecosystems that have already been long devoid of apex predators and many other consumers lower in the food web. Another study (Eriksson et al. 2009) showed that declines in predatory fish were promoting blooms of macroalgae in the Baltic Sea through cascading effects down the food web. Through surveys they showed that macroalgal cover was highest when abundances of large piscivorous fish were low, which led to higher abundances of smaller fish that feed on invertebrate grazers. Further manipulative experiments supported the notion that these predators when abundant exerted a strong top-down forcing on the food web (Eriksson et al. 2009).

21.5 Bottom-Up Versus Top-Down Control in Marine Coastal Ecosystems

There are an overwhelming number of studies focusing on bottom-up versus top-down controls of primary producer biomass and community structure in marine coastal waters (Hauxwell et al. 1998; Lapointe 1999; Balducci et al. 2001; Lotze et al. 2001; Smith et al. 2010; Martinetto et al. 2011; Fox et al. 2012). Marine communities are, in general, naturally regulated by bottom-up and top-down forces; however, the increase in anthropogenic activities in the coastal zone has influenced the relative strength of bottom-up and top-down controls on these communities. In many instances, increased nutrient inputs seem to be the main driver of macroalgal blooms (Valiela et al. 1997; Hauxwell et al. 1998; Lapointe 1999), while in others changes in grazing pressure are thought to be responsible (Hughes 1994; Smith et al. 2010).

In order to determine the relative influence of these two factors, many experimental manipulations of nutrients and grazing have been carried out in marine habitats under a range of different in situ conditions. Recent metaanalyses by Burkepile and Hay (2006) and Gruner et al. (2008) have compiled the results of these experimental studies to see whether any general patterns can be deduced regarding the relative influence of top-down and bottom-up controls on these ecosystems. They found that in most cases nutrients and grazers independently affected producer biomass, but that the relative role of top-down versus bottom-up control is context dependent, that is, it may differ by latitude, by type of marine habitat, by the functional groups of algae or type of grazers in the system, by the productivity of the ecosystem, or by the sampling method of producer response (Burkepile and Hay 2006; Gruner et al. 2008). They also found that in some cases there were interactive or synergistic effects, in which nutrient enrichment in the absence of herbivores showed the highest productivity and percent cover of macroalgae (Gruner et al. 2008; Burkepile and Hay 2006).

21.5.1 Latitudinal Patterns

Most reports from temperate latitudes addressing the forces behind macroalgal blooms appear to suggest that nutrients were involved (Baden et al. 1990; Valiela et al. 1992; Sfriso et al. 1992; Raffaelli et al. 1998), with the exception of rocky shores (Lubchenco 1978; Lotze and Worm 2000). Similar studies from tropical latitudes place less emphasis on nutrients and suggest large impacts of grazing on macroalgal blooms (Lewis 1986; Hughes 1994), but opinions differ (Lapointe 1997; Littler et al. 2006). The metaanalysis of Burkepile and Hay (2006) showed that in tropical marine habitats, macroalgae responded independently to both nutrient enrichment and herbivore removal by increasing biomass or cover. Nutrient effects were, however, smaller than the grazing effects, and only important when herbivores were absent. This was not the case for temperate marine habitats, which tended to vary in the relative effects of bottom-up and top-down control based on the nutrient status of the system. In high nutrient environments bottom-up effects were stronger, while in low nutrient environments top-down effects were more significant (Burkepile and Hay 2006).

One of the main explanations for these latitudinal differences in the control of macroalgal blooms is the types and sizes of grazers and their grazing rates. Other possible explanations may be the extent of nutrient loading, the macroalgal taxa involved in different systems, the length of the growing season, and the range in light intensity in temperate versus tropical coastal waters.

21.5.2 Dominant Control in Different Habitats

In this section, we provide some key examples from the literature defining the relative roles of bottom-up and top-down controls within different marine habitats, including estuaries and coastal bays, coral reefs, and intertidal and subtidal rocky shores. Through these examples, we show the variation in macroalgal responses to their controls, and also try to include some of the studies, which have paved the way or stimulated the debate in this field.

21.5.2.1 Estuaries and coastal bays

The relative roles of bottom-up and top-down controls in estuarine systems have been thoroughly studied due to the high degree of disturbance found in these ecosystems as a consequence of coastal urbanization and development. This overdevelopment leads to higher nutrient inputs from point and nonpoint sources of wastewater and fertilizers into coastal waters, while wetlands and forests that generally buffer and act as a filter along the coastline are being removed at alarming rates. Most sites receiving high nutrient enrichment generally are found to be bottom-up controlled, whereas undisturbed low nutrient environments are often found to be top-down controlled (Hauxwell et al. 1998; Burkepile and Hay 2006; Fox et al. 2012).

This general model of the relative importance of bottom-up and top-down controls on macroalgal blooms in estuaries is again exemplified by the Waquoit Bay example. Waquoit Bay macroalgal blooms are stimulated by high nitrogen loading to its receiving subestuaries (Valiela et al. 1997; Hauxwell et al. 1998; Fox et al. 2008). In the high nitrogen loaded sites of Waquoit Bay, macroalgal growth rates and biomass were highest (Hauxwell et al. 1998). Additionally, more frequent hypoxic events lowered the abundance of small crustaceans, the dominant grazers, and therefore, grazing rates were too low to compensate for the increase in algal biomass (Hauxwell et al. 1998; Fox et al. 2009, 2012). In contrast, in the low nitrogen loaded site macroalgal growth rates and biomass were lower, grazers were very abundant, and macroalgae were easily controlled by consumption rates (Hauxwell et al. 1998; Fox et al. 2009, 2012).

Another well-studied case of bottom-up and top-down controls of macroalgal blooms is that of Venice Lagoon. In the 1970s and 1980s, the lagoon received inputs of nutrients from urbanized areas in and around Venice from agricultural, industrial, and treated and untreated sewage effluent sources (Sfriso et al. 1992). With high nutrient loading came noticeable changes in benthic community structure driven by large blooms of *Ulva rigida* and other green macroalgae (Sfriso et al. 1987, 1992). Between 1987 and 1998, macroalgal standing crop in Venice Lagoon declined to only 1.6% of what was present in 1987 (Sfriso et al. 2003). This dramatic reduction was initially thought to be due to a combination of changes in climate, sedimentation fluxes, and management of nutrient loading entering the lagoon. Additionally, as macroalgal growth declined, fewer anoxic events allowed for the recovery of invertebrate grazers, which were able to help control macroalgae blooms from the top-down (Balducci et al. 2001).

Other biotic and abiotic factors, however, may affect the relative roles of bottom-up and top-down controls of macroalgal communities in estuarine systems. For example, reproduction and recruitment of early life history stages of macroalgae may respond differently under nutrient enrichment and grazing pressure than adult life stages (Lotze et al. 1999, 2000, 2001; Lotze and Worm 2000). Lotze et al. (1999) found that the bottom-up and top-down controls on early life stages may act as a bottleneck for bloom-forming species of macroalgae in some cases. Lotze et al. (2001), however, showed that total recruit density of ephemeral bloom-forming macroalgae *Ulva* and *Pilayella* spp. in the Baltic Sea was positively influenced by nutrient enrichment, while grazing only limited recruitment and growth of the more palatable of the two species without changing the total recruitment (Lotze et al. 2001).

Macroalgal community structure may also influence the strength of bottom-up and top-down controls. In the presence of canopy-forming macroalgal species, such as *Fucus vesiculosus*, the response of ephemeral algae to nutrients was found to be limited by as much as 90% compared to those without canopies due to a reduction in light availability (Eriksson et al. 2007). In contrast, the presence of epiphytes growing on macroalgae may actually stimulate macroalgal growth if epiphytes are preferentially consumed by grazers (Kamermans et al. 2002; see also Chap. 11 by Potin). Furthermore, on a smaller spatial scale, the presence of grazers within the macroalgal canopy may also be an additional source of nutrients through their excretion (Taylor and Rees 1998, see also Chap. 4 by Gordillo).

Hydrodynamics can also alter the strength of bottom-up and top-down controls on a system. For example, in Mondego Estuary, Portugal, mitigation measures to improve the hydrodynamics of the estuary have been found to alleviate macroalgal blooms occurrences caused by high nutrient loading by increasing the circulation and diverting inflow of nutrient-rich waters (Lillebø et al. 2005). In San Antonio Bay, Argentina, high nutrient loads enter the bay exposing macroalgae to elevated nutrient concentrations during low tide and supporting a large macroalgal biomass (Teichberg et al. 2010; Martinetto et al. 2010, 2011). Additionally, large tidal flushing helps to remove anoxic waters and nutrients from the system, minimizing hypoxia-related stress on grazers and negative cascading effects up the food web (Martinetto et al. 2010, 2011). Therefore, the high biomass of nutrient-rich macroalgae can provide a large quantity of food with higher nutritional quality to grazers and support higher grazer abundances (Martinetto et al. 2010, 2011).

21.5.2.2 Coral reefs

In the last four to five decades, there has been an increasing trend of macroalgal blooms in coral reefs coinciding with a decrease in coral cover (Hughes 1994; McManus and Polsenberg 2004; Nugues and Bak 2008). This shift from coral to macroalgal-dominated reefs, known as coral–algal phase shifts, has stimulated much of the debate in the relative role of top-down and bottom-up controls in marine habitats. Some studies have shown that the removal of the dominant herbivores, through overfishing or natural causes, has been more important as a control on macroalgal growth than nutrient enrichment (Hughes 1994; Hughes et al. 1999; Burkepile and Hay 2006; Sotka and Hay 2009). Others state that recent increases in nutrient inputs from land to coastal reefs have triggered macroalgal blooms (Lapointe 1997; Lapointe et al. 2005a, b). And then there are those studies that support both top-down and bottom-up controls as important influencing factors (McClanahan et al. 2003; Littler et al. 2006; Smith et al. 2001). In this chapter, we do not attempt to provide a comprehensive review of the current extensive literature on coral–algal phase shifts in coral reefs, but rather focus on a few specific studies that examine the effects of top-down and bottom-up controls on macroalgal growth.

In Hughes (1994), one of the first long-term studies of coral reef decline in the Caribbean reported large-scale natural and human disturbances were linked to coral–algal phase shifts. In most of the reefs around Jamaica, the driving factors of these phase shifts were thought to be the increase in human population, which drove an increase in overfishing, followed by the mass mortality of the sea urchin *Diadema antillarum*. Without herbivorous fish and *D. antillarum*, the dominant grazers of macroalgae on the reefs, blooms of filamentous macroalgae began to overgrow corals, which were then replaced by late successional stage species, such as *Dictyota*, *Lobophora*, *Halimeda*, and *Sargassum* spp. These macroalgae inhibited coral reef recovery by effectively competing for open space needed for recruitment of coral larvae (Hughes 1994). Lapointe (1997) introduced another potential trigger of macroalgal blooms on these Jamaican reefs by showing that bottom-up control also played a role. It was demonstrated that dissolved inorganic nitrogen from wastewater entered the reefs through groundwater discharge and elevated reef nutrient water concentrations sufficiently to sustain macroalgal blooms in these habitats (Lapointe 1997). These studies spurred a debate as to the relative role of bottom-up and top-down controls on coral reefs (Hughes et al. 1999; Lapointe 1999).

Since this debate began, a few studies have demonstrated how both top-down and bottom-up controls can be important. Littler et al. (2006) developed a conceptual model, the Relative Dominance Model, to describe the process of bloom formation on reefs under independent and combined factors of nutrients and grazing pressure. Results of manipulative experiments, bioassays, and surveys of communities showed that: (1) under reduced nutrients alone fleshy algae grow when herbivory is low, (2) under high herbivory alone fleshy algae grow when nutrients are high, (3) reduced nutrients and high herbivory prevent blooms of macroalgae (Littler et al. 2006). It has also been found that different controls are important for different groups of algae; for example, McClanahan et al. (2003) found that turf algae were positively affected by nutrients and negatively affected by herbivory, while frondose brown algae grew better under low nutrients and low herbivory. Vermeij et al. (2010) also found that turf algae can overgrow corals under high nutrients, but that herbivores are not able to control their growth under these conditions.

Despite the evidence that bottom-up control does play a role in triggering macroalgal bloom formations on reefs, the majority of studies support that top-down control is the primary driving factor (Thacker et al. 2001; Burkepile and Hay 2006; Sotka and Hay 2009). A recent study in a pristine fisheries management area along a Hawaiian reef revealed that in the absence of herbivores, fleshy macroalgal abundance was higher than in any other treatment, while in the presence of herbivores corals and crustose coralline algae were more abundant (Smith et al. 2010). The effects of nutrient enrichment supported slightly higher macroalgal percent cover than in nonenriched treatments, but the species composition depended on the herbivore treatment. After reexposure to natural conditions, the effects of enrichment and herbivore absence disappeared over a relatively short time frame, supporting the notion that increasing herbivore populations is critical to reduce macroalgal blooms on reefs (Smith et al. 2010).

Based on the variable results of studies examining top-down and bottom-up controls of macroalgal blooms on coral reefs, the relative role of these controls is still not fully resolved. Only through larger scale changes in fishing regulations and better management of nutrient inputs to coastal reefs will we be able to better distinguish which of these or the combination of both is the causal factor.

21.5.2.3 Rocky Intertidal and Subtidal Ecosystems

Much of the knowledge defining the role of top-down controls on macroalgal community dynamics began with the well-known classical ecological studies in rocky intertidal and subtidal communities (Paine and Vadas 1969; Lubchenco 1978, 1983; Estes et al. 1978; Lubchenco and Menge 1978). These studies showed how removal of the dominant grazers or predators influenced macroalgal diversity and community structure directly or indirectly through cascading effects from the top-down. In the experimental study by Paine and Vadas (1969), the removal of the sea urchin *Strongylocentrotus purpuratus* resulted in an increase in the biomass of brown algae (*Hedophyllum sessile* and *Laminaria complanata*) in intertidal pools and subtidally on the rocky coast of Washington, USA. Lubchenco (1978) showed that when snails were removed from tide pools where *Chondrus crispus* dominated, green ephemeral species settled quickly and outgrew *C. crispus*.

Only more recently has the role of bottom-up control, in terms of nutrient supply, been explored in rocky shores (Menge 1992; Nielsen 2003; Bokn et al. 2003; Korpinen et al. 2007a, b). A review by Menge (1992) discusses some of the reasons the role of bottom-up controls on rocky shores has been neglected for so long, including the overemphasis of physical stress in these environments, logistical and methodological constraints of experiments, and different training backgrounds of marine benthic ecologists. Possible explanations of how nutrient enrichment cascades up the food web and affects the community structure of rocky shores were also discussed using a case study along the Oregon Coast. In this environment, nutrient loading from upwelling was thought to increase primary production and lead to higher abundances of filter-feeding prey that then supported higher abundances and feeding rates of predators (Menge 1992). Further studies have also shown that increased phytoplankton due to upwelling events and nearshore hydrography drives this bottom-up regulation of the benthic community (Menge et al. 1997).

The relative effects of bottom-up and top-down control on the rocky shore macrophyte community along the same rocky shoreline were later experimentally tested in intertidal pools by Nielson (2003). Small increases in nutrient supply strongly increased the total percent cover of macroalgae and the diversity of benthic macrophytes under low herbivore abundance, but not under high herbivore abundance. This response in the macrophyte community was primarily due to an increase in the functional group of corticated algae. The results of this study suggest that open-coast marine intertidal communities are more sensitive to fluctuations in nutrient regimes than previously thought, and that nutrient effects are likely to be amplified where consumers are overexploited or naturally low in abundance (Nielsen 2003).

In both the above cases, bottom-up control of intertidal communities was driven by natural sources of nutrients from upwelling events rather than anthropogenic sources. However, other scientists have linked changes in the macroalgal community structure of rocky shores to coastal eutrophication, where macroalgal assemblages nearer to urbanized areas consisted of higher abundances of the opportunistic chlorophyte *Ulva* spp. than in control sites (Díaz et al. 2002; Worm and Lotze 2006). Overall the consensus is that top-down controls are dominant on rocky shores but that bottom-up controls can interact with top-down controls to change patterns in macrophyte community structure and food web interactions.

21.6 Conclusion

There may be no general solution to the bottom-up top-down debate in macroalgal communities, but rather different responses based on species or functional groups, physical and chemical environments, and types of grazers. The fact that so many rigorous experimental studies have found conflicting results shows that both factors are important under different circumstances and often interact simultaneously.

The human population is projected to steadily increase, which will result in further anthropogenic pressure on coastal marine systems. It is likely that nutrient loading rates and fishing pressure will intensify, despite management efforts. The impacts of nutrient loading and overfishing will also be exacerbated by other global changes, such as rising seawater temperatures, sea level rise, and ocean acidification. Nutrients in combination with warmer waters may promote more occurrences of macroalgal blooms, as photosynthesis, growth rates of macroalgae, and recruitment are thought to be positively affected by an interaction of these factors (Longstaff et al. 2002; Lotze and Worm 2002; Bintz et al. 2003; Tsai et al. 2005). Additionally, enhanced CO_2 conditions have been shown to benefit some ephemeral bloom-forming macroalgal species over other slower growing species (Gordillo et al. 2001; Wootton et al. 2008), while negatively impacting many benthic invertebrates (Fabry et al. 2008). Additionally, the increase in invasions by nonnative macroalgal species to new coastal habitats may promote blooms of macroalgae that are better adapted to changing environmental conditions (Thomsen et al. 2006). Cascading effects up or down the food web and, thus, the strength of bottom-up and top-down controls acting on macroalgal communities will likely be altered due to these shifts in species composition and environmental change (Fox et al. 2010).

Management of all aspects (nutrients, fishing, habitat protection, reduction of CO_2 emissions) is important, and choosing one management practice over another will not be successful at controlling macroalgal blooms. The management and removal of nitrogen and phosphorus is necessary as a first step. Wastewater treatment plants and improvements in septic systems have shown significant positive effects on water quality through the removal of the bulk of nutrients prior to entering the coast or groundwater. Reduction of fertilizer use and phosphate-free detergents can also reduce the amount of nutrients entering these systems. Preservation and restoration of wetlands will help to filter nutrient inputs before they enter rivers and coastal waters. Additionally, improving hydrodynamics of low-flow systems by increasing tidal flushing could help to mitigate nutrient effects. Increases in fishing regulations and protected areas with no take zones may help to increase fish and invertebrate populations. This will impact food web communities in multiple ways and will strengthen top-down controls on macroalgal growth.

In many cases, these management practices may not be enough to facilitate recovery of marine habitats to their natural state prior to disturbances, and much is still unknown as to how bottom-up and top-down controls will interact with future global change projections. It is very likely that macroalgal blooms will continue to become more frequent and severe in coastal systems before conditions improve. A better understanding of how these controls will interact under predicted future conditions is critical to develop tools to mitigate these changes.

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Part V
Aquaculture and Economical Importance of Seaweeds

Chapter 22
Seaweed and Man

Cornelia M. Buchholz, Gesche Krause, and Bela H. Buck

22.1 Aquacultural Production of Seaweeds and Its Economic Relevance

22.1.1 Introduction

Despite an Asian aquaculture tradition of many centuries, aquatic farming on the global scale is still a young sector of food production that has grown rapidly in the last 50 years. Seaweeds, a colloquial but widely used term for macroalgae, play an important role in this business which remains a growing, vibrant, and important production sector for healthy human food.

As archaeological investigations in Chile testified, seaweeds have been used by humans for about 14,000 years (Dillehay et al. 2008). According to earliest written records, they were consumed in Japan during the Asukaand Nara Era approx. 1,500 years ago. Even food products directly made from seaweeds have a long

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tradition and can be traced back to the fourth century in Japan and the sixth century in China (Tseng 1987; Mc Hugh 2003). Exclusively wild seaweed was used, which limited it as a food source up to the Middle Ages. Later, during the Shogun regime in the Tokugawa Era (1600–1800 AD) fishermen constructed artificial substrates for fish farming which also allowed various seaweed species to grow upon. Ever since, seaweeds have been cultivated in the sea (Tamura 1966). Increasing demand over the last 50 years has outstripped the ability to supply the required biomass from natural (wild) stocks which triggered a dramatic growth of seaweed production from aquaculture sources.

Following Bartsch et al. (2008) farmed seaweeds are used for various applications, as food as well as in the textile, pharmaceutical, cosmetic, and biotechnological industry. As a source of food for human consumption seaweeds can be used in different forms – for instance in salads, sushi recipes, or as various food additives. Other purposes are the use on the health market advertising its minerals and enzymes. Industrial macroalgal use includes the extraction of phycocolloids and biochemicals (Sahoo and Yarish 2005; Pereira and Yarish 2008). A wide range of potential utilizations of seaweeds and/or algal compounds are referred to in Sect. 22.3.

The accessibility and reliability of data on "aquatic plants" (FAO classification) concerning collection from the wild as well as aquaculture production is still not sufficiently consolidated and spread. Acknowledging the shortcomings the Food and Agriculture Organisation of the United Nations (FAO) has continually improved its assessment of the available sources of information, evaluated and updated them, and with addition of some educated estimates published annual statistics that may well serve as a useful guide to world seaweed production and marketing. The latest report by the FAO on "The State of World Fisheries and Aquaculture 2010" contains data up to 2008 (FAO 2010a). Including the latest available data from 2009 (FAO 2011b), we can show the state and development of this industry up to that year and present the new numbers adjusted by the FAO for the period 1997–2005 (Fig. 22.1) after China revised its production statistics based on its Second National Agricultural Census 2007 (FAO 2010–2011). Since China by far runs the most intensive aquaculture business worldwide, numbers on global aquaculture production had to be decreased by about 8% (FAO 2011b).

22.1.2 Aquaculture Production of Seaweeds

Farm production of "aquatic plants" has permanently been expanded since 1970 with an average annual growth rate of 7.7%. It is overwhelmingly dominated by macroalgae (seaweeds) while cultivation of microalgae on a large commercial scale is still in its infancy.

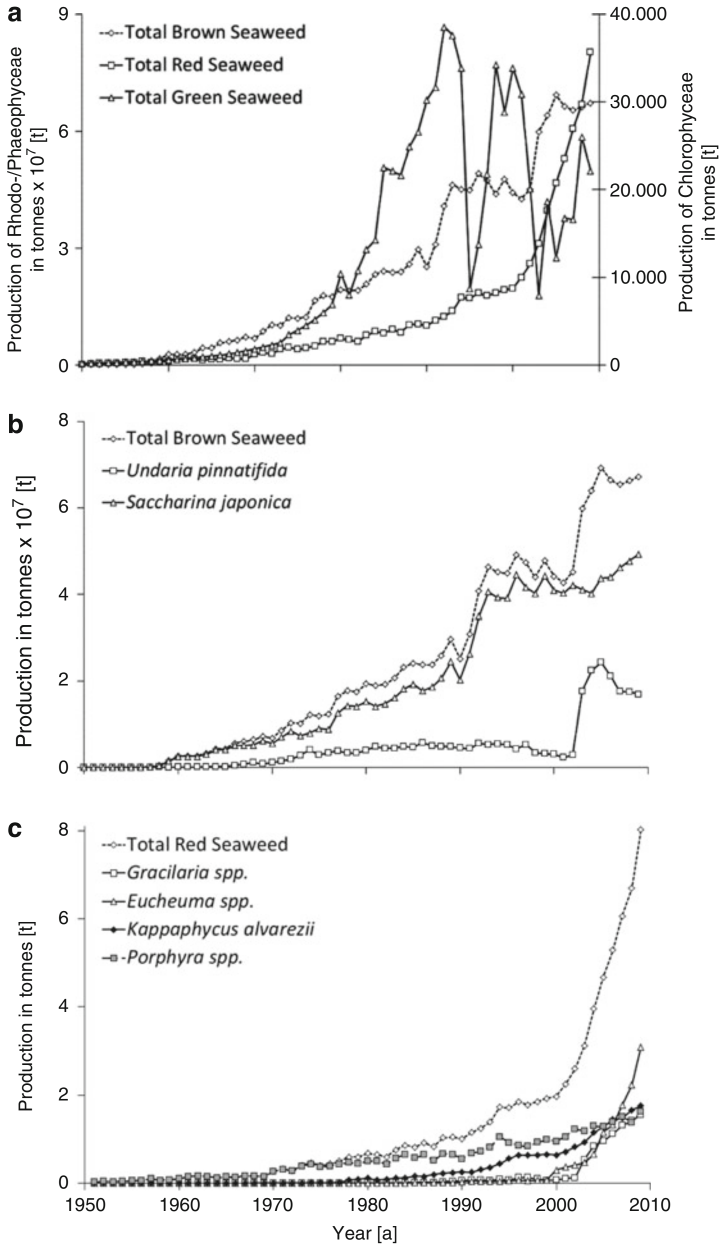

Fig. 22.1 (continued)

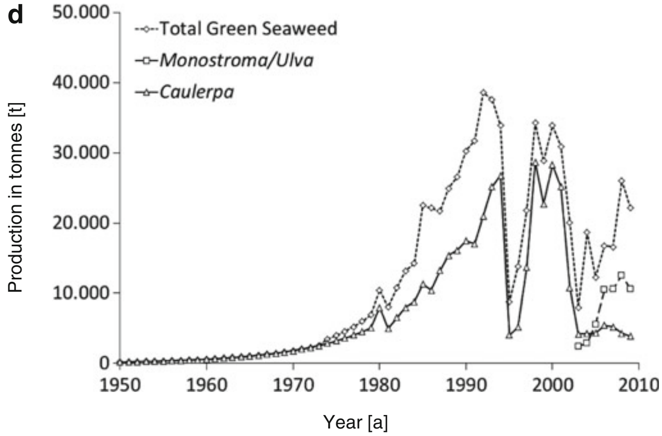

Fig. 22.1 Global production of seaweeds over time according to FAO (2011a). (**a**) Overview of the three groups of seaweeds. (**b**) Global aquaculture production of brown seaweeds with the most important crops used for food and production of alginate. (**c**) Global aquaculture production of red seaweeds comprising the most important agarophyte *Gracilaria*, the carageenophytes *Eucheuma* and *Kappaphycus*, and the high value food algae of the genus *Porphyra*. (**d**) Global aquaculture production of green seaweeds showing "green nori" as a relatively new crop among the most important algae sold for food

22.1.2.1 Species Variety

In 2009, the greatest biomass of cultured species (Fig. 22.2) were the popular food kelps *Saccharina japonica* (formerly *Laminaria japonica*), named "Kombu," with 4.9 million tons annually, and *Undaria pinnatifida,* also known as "Wakame," with 1.7 million annual tons. Among the rhodophytes that are produced the carrageenophytes *Kappaphycus alvarezii* and *Eucheuma* spp., both known as "Cottonii," (4.8 million tons), the red agarophytes of the genus *Gracilaria*, called "Ogonori" in Japan (296,000 tons), and the red *Porphyra* spp. valuable as food alga "Nori" (1.6 million tons) are particularly important. Other species like *Palmaria*, *Chondrus*, or the green *Ulva*, etc. are produced to a minor extent (FAO 2011a).

22.1.2.2 Biomass Yield and Value

To date and worldwide more than 14.7 million tons of seaweeds (miscellaneous vascular flowering plants like Zostera spp. or eel grass etc. not included) are commercially produced, 6% collected from wild stock, 94% farmed. The seven top seaweed farming countries deliver 99.95% of the global farmed volume and are all situated within Asia: Most productive is most productive is China with 54% followed by Indonesia with 20% and the Philippines with 12%. Chile is the most important seaweed farming country outside Asia having produced 88,147 tons in 2009, which is more than 99.9% of America's (north and south) total volume.

Fig. 22.2 Examples of macroalgae grown in aquaculture. (**a**) *Solieria*, a carrageenophyte; (**b**) *Chondrus crispus* "Irish Moss" carrageenophyte; (**c**) *Palmaria palmata*, used as feed for abalone; (**d**) *Ulva lactuca*, used for bioremediation (uptake of excess nutrients) and feed; (**e**, **f**) *Saccharina latissima*, after 9 months in tank culture and (**f**) phylloids drying for storage demonstrating how evenly they are grown. (Photographs **a**, **b**, **c**, **e**, **f** by K. Lüning with permission)

Next in the ranking according to production volume are countries mostly from Africa (e.g., Tanzania, Madagascar, South Africa, and Namibia) with 108,400 t in 2009 and Western Europe (e.g., Spain, France, Italy, and the Russian Federation), which are responsible for the remaining biomass production volumes. Finally, the Pacific Ocean Islands grow just a small amount of seaweed and produced 2,377 tons in 2009 (Fiji, Kiribati, and Solomon Islands) (FAO 2011a, 2010b).

22.1.3 Methods of Production and Technical Design

Quite a great amount of preliminary observations and experimental setups are necessary for a commercially successful cultivation of seaweeds. To pick the right choice of species thorough knowledge of the alga's often complicated life cycle and a good control of the different life stages are crucial. Likewise local weather conditions, the temperature range, wave action, currents, tidal amplitude, and salinity levels must be appropriate for the respective target species. Further factors to consider are nutrient supply in the water, water depth, and transparency to maintain beneficial irradiance levels, which may, in the case of shallow water farming, also be influenced by the color and composition of the bottom sediments. Moreover, ideally, grazers should not be found in the vicinity of a farm and the presence of epiphytes or other unwanted macroalgal species competing for light and nutrients should have been tested before a commercial farm is ventured (see also Chap. 11 by Potin).

Since the worldwide demand for seaweeds and their products could not be met by simple collection from natural populations, several decades of effort have gone into farming (Tseng 1984, 1987). A considerable number of technical variations in cultivating seaweeds are presently used depending on species, local conditions, and experience (Pereira and Yarish 2008). Meanwhile cultivation methods comprise not only single species cultures but also integrated multi-trophic aquaculture (IMTA; Chopin et al. 2008; Buschmann et al. 2008).

22.1.3.1 Monocultures of Seaweeds

Basically, seaweeds are either "seeded" on ropes or nets (e.g., *Porphyra)* or thallus fragments are fastened on or pinched into ropes, which are subsequently fixed to various suspended or floating culture structures (e.g., *Gracilaria*). From Chile a system to anchor *Gracilaria* cuttings in the sand is known and has also been successful (Trono 1990; Pereira and Yarish 2008; FAO 2011c: National Aquaculture Sector Overview—NASO). Paddle wheel ponds that keep algae floating and moving are a suitable device to grow the green *Ulva* to large quantities (Chopin et al. 2008; Butterworth 2010).

"Nori" production comprising several species of the genus *Porphyra* is a big business worldwide valued at US$ 1,400 million in 2008 according to the FAO statistical yearbook 2010 (FAO 2010b). After about 300 years of culture efforts dependent on natural seeding, Baker (1949) discovered the conchocelis phase of this genus. Only then could the present-day effective multistage culture system be established (Pereira and Yarish 2008, 2010). *Porphyra* is mainly cultivated in China, Japan, and Korea: Mollusk shells, mostly of oysters, are seeded with diploid carpospores from preselected thalli and kept in large shallow indoor tanks for approx. 5 months until under nutrient, temperature, and light control conchospores are released by the conchocelis filaments. Appropriate spore density and agitation of the suspension facilitate even settlement on collecting nets. After germination, grow-out of the thalli takes place in relatively shallow bays, nets fixed, semi-floating, or floating (Sahoo and Yarish 2005; Pereira and Yarish 2010). Fixed or semi-floating, the alternation of immersion and desiccation with the tide is guaranteed helping to avoid diseases caused by fungi or bacteria, reducing epiphytic diatoms and improving the taste. Floating nets can be kept over slightly deeper water (10–20 m), thereby extending the farming area. However, a nursery system must be included that periodically dries the nets and hardens them (Pereira and Yarish 2008, 2010). It is also possible and even improves the quality of the final product to carefully freeze the nets with young thalli and store them at −20°C for later grow-out (FAO 2005–2011a). Depending on the species it takes 40–50 days at sea, for *P. haitanensis* and *P. yezoensis*, respectively, before the first crop can be attained. Six to eight harvests are possible during 5 months of cultivation (Pereira and Yarish 2010).

The species with the highest production is the brown alga *Saccharina japonica* (formerly *Laminaria japonica*), “kombu.” 4.9 million tons of kombu were produced in 2009, 84% of it grown in China, where the species is not endemic, but was introduced in 1927 (Tseng 1987; Lowther 2006). Conventional “2 year cultivation” of *S. japonica* took a period of 18 months at sea with at least another 2 months for “seeding,” which resulted in relatively high prices for the product (Ohno 1993). “Cultivation by transplanting” uses natural *Saccharina* sporophytes either washed ashore or manually thinned out. As the activity of the meristem increases in late winter to early spring, new haptera are easily formed and allow a new attachment on ropes during this time. Time from transplantation to harvest lasts 12–18 months (Ohno 1993). Only 12 months are needed for the widely applied so-called forced-cultivation technique (Hasegawa 1971; Ohno 1993; Critchley and Ohno 1997; Sahoo and Yarish 2005). This became possible due to scientific control of the entire biphasic life cycle, where indoor facilities are necessary to manage the labor and cost-intensive “seedling phase” (Tseng 1989; Mc Hugh 2003; Chen 2006). A large independence of naturally available seedstock could be attained by detaching *Laminaria* frond fractions from the meristem (Buchholz and Lüning 1999; see also Lüning et al. 2000; Pang and Lüning 2004). Meiospores are artificially released from sporogenous thalli, germinate to microscopic gametophytes, form zygotes, and eventually produce young sporophytes that stick to ropes. In “the grow-out phase” (Tseng 1989), culture ropes with juvenile sporophytes are transferred to the open sea where they grow to a frond length of approx. 1–2.5 m, depending on the species. If the predicted shift of biogeographic areas becomes true (see also Chap. 18 by Bartsch et al.), aquaculture of *S. japonica,* as an example, may be strongly impaired in that the space and the period for grow-out in coastal waters are reduced. Young seedlings do not tolerate more than 20°C and fronds have to be harvested at ≤21°C, because they start to rot at higher temperatures (FAO 2005–2011b) .

The most common design for grow-out of Laminariales in the open water is a longline system of horizontal ropes parallel to the sea surface with anchoring weights to stabilize the entire system and with buoys to provide flotation. Combining vertical arrangement of seeded culture lines as the first step and later suspension and lifting of these lines into a horizontal position overcomes first overexposure, then shading problems in growing sporophytes, while reducing effects of cross currents and storms on only horizontally attached lines (FAO 2005–2011b). From the various methods (e.g., Holt and Kain 1983; Kawashima 1984; Kain and Dawes 1987; Dawes 1988; Kain 1991; Merrill and Gillingham 1991; Critchley and Ohno 1997; Buck and Buchholz 2004), the locally appropriate one has to be chosen for the special conditions of a given farming site.

Longline systems installed in harsh offshore conditions, to where farms could be expanded, were not robust enough as there is a considerable stress on support material and algae (Buck 2004; Buck and Buchholz 2004). Among the various suggestions for technical structures that have been made (Polk 1996; Hesley 1997; Stickney 1998; Bridger and Costa-Pierce 2003) a ring design did withstand strong currents and wind waves and is still the most promising (Buck and Buchholz 2004). The idea of utilizing the grounding structures of offshore wind generators for the fixation of aquaculture systems is intriguing (e.g., Buck 2002; Krause et al. 2003; Buck et al. 2004) and the first experiments on *Laminaria* species show that adapted to strong currents as young individuals, they grow well at exposed sites (Buck and Buchholz 2005).

The cultivation of seaweeds at sea or in ponds flushed by incoming seawater has lately been supplemented or completely exchanged for land-based tank cultivation for smaller rhodophytes and chlorophytes (see Sect. 22.1.3.2) as well as large kelps. Lüning and Pang (2003) kept free floating sporophytes of laminarians or *Palmaria palmata* circulating in the water agitated by air. The tanks allowed a high cultivation density of 10 kg m^{-2}, since shading was amended by the continuous turnover of fronds toward the light. Uniform exposure to nutrients was likewise facilitated and the infestation with epiphytes was kept very low (Ryther et al. 1979; Bidwell et al. 1985). The Lüning and Pang (2003) system was additionally supported by a continuous short day treatment. The same short day treatment (8 h light) using outdoor tanks with automatic blinds resulted in prolonged growth activity of *Laminaria digitata* that also seemed to deter epiphyte settlement (Gómez and Lüning 2001). The experience gained in tank cultivation is a valuable basis for some of the internationally developing integrated mariculture systems (see citations in Neori et al. 2004, p. 376; Abreu et al. 2011; Pereira et al. 2011).

The world population recently reached the seven billion mark and a sustained or rather growing supply of protein from aquatic animals is highly desirable. Concomitantly there is an increasing concern about the negative consequences of intensive and constantly spreading aquaculture of fish, shrimps, and mollusks. Therefore, the remediation of negative consequences has been a field of intensive research during the last decade. Two ecologically sensible strategies to meet the requirements for more space allotted to aquaculture have been and will continue to be tested: One is the offshore aquaculture that to date seems very expensive and technically demanding, but will allow considerable mass production. The other is the very promising but likewise complicated Integrated Multi-Trophic Aquaculture (IMTA) approach.

22.1.3.2 Integrated Multi-Trophic Aquaculture (IMTA)

Extensive polyculture pond systems with organisms of several species in the same water body have traditionally been applied in Asian countries and were based on trial and error. Only since the 1970s, a more systematic approach has resulted in the development of integrated intensive land-based mariculture systems (Ryther et al. 1979). The aim of IMTA is the creation of a manageable small ecosystem with several species of different trophic levels combined in one system in the right proportions, each utilizing waste products or the biomass generated by another member of the system. All of the individual components must be marketable since the commercial viability is an important factor of any such IMTA design (Chopin et al. 2008). If the benefits for the environment were accounted for, the value of IMTA production systems would be highly increased and political support for the development of these structures would mirror this.

Neori et al. (2004, 2007) argued that seaweed-based integrated aquaculture systems will most probably facilitate the expansion and sustainability of the worldwide aquaculture industry. Nevertheless, the major aim of global aquaculture enterprises is the production of fish, shrimp, or shellfish protein. With the dwindling of wild resources through overfishing there is an ever growing demand for those products. At the same time the demand for certain seaweeds for human consumption or animal feed or else for algal ingredients (mainly phycocolloids) has to be met and is already a large market, worth 22.4 billion US$ in the year 2008 (FAO 2010b).

Since the culture of fed species like fish or shrimp inevitably results in eutrophication of the adjacent waters (Stead and Laird 2002; Fei 2004; Sanderson et al. 2006; Troell et al. 1999, 2003), a bioremedial complementary culture design makes sense for environmentally protective reasons. Simultaneously the biomass of carefully chosen extractive and marketable species could at least partly counterbalance the considerable costs for fish or shrimp feed (Neori et al. 2004; Abreu et al. 2009). Moreover, there are oligotrophic seawater conditions, like in Israel or Australia, that do not allow the growth of algae and it makes sense to try intelligent new aquaculture approaches under these circumstances (Schuenhoff et al. 2003; Butterworth 2010; Neori et al. 2004).

An encompassing review of the multiple IMTA activities is found in Barrington et al. (2009) for temperate and Troell (2009) for tropical regions of the world. Potential candidates for integrated systems are not only the hitherto monocultured and expensively fed fish and crustaceans, filter-feeding bivalve or herbivore mollusks (*Haliotis*), and more than 20 species of seaweeds but also echinoderms and polychaetes. Presently existing IMTA systems usually contain no more than three components at different trophic levels. One is fed fish or shrimp, one extracting organic bound nutrient particles, either feed leftovers or feces, and one, seaweeds, extracting the effluents utilizing inorganic nitrogen and phosphate for growth. In a Sustainable Ecological Aquaculture effort Cascadia SEAfood even integrates sablefish with two species of bivalves, kelp, and sea urchins that feed on the fouling organisms on cages, their gonads being offered to seafood gourmets (Cross 2010; Cook and Kelly 2007). In the case of an abalone farm in South Africa, the resulting seaweed crop of *Ulva lactuca* can partly be used for feeding the abalone (Nobre et al. 2010; Robertson-Andersson et al. 2008). Since it is known that *Ulva* synthesizes more protein ($>40\%$ dw^{-1}) with higher ammonia-N in the water, it turns out to be a valuable feed allowing *Haliotis* to grow significantly faster than with Ulva kept in low nitrogen concentrations and containing only 12% protein (Shpigel et al. 1999).

While *Ulva* spp. with their thin thalli and large surface-to-volume ratio are perfect inorganic extractors their biomass does not realize a high price. Therefore, commercially valuable red algae like *Porphyra* (nori), *Gracilaria* (as an agarophyte), and *Kappaphycus* (as a carrageenophyte) are being tested in IMTA systems (Chopin et al. 1999; Abreu et al. 2009, 2011; McVey et al. 2002; Pereira and Yarish 2010; Rawson et al. 2002; Robertson-Andersson et al. 2008; Lombardi et al. 2006). Depending on the region, particularly those with pronounced seasons, seaweeds in IMTAs may have to be exchanged for other species in the course of the year, which requires additional engineering efforts to suit each species' requirements. There are for example different demands of red algae versus brown kelps concerning surface area, water flow rates, and nutrient exchange, etc.

Owners of profitable finfish or shrimp cultures are not necessarily concerned about eutrophication of the environment and have to be convinced that no diseases are introduced by co-cultured organisms (Troell et al. 2003). It needs the owners' consent to use existing fish or shrimp cultures to establish an IMTA system: In open sea, but nearshore systems, different components of an IMTA can simply be placed in each other's vicinity with mutual beneficial effects provided local currents and other water dynamics allow sufficient exchange between them (Abreu et al. 2009; Sanderson 2009; McVey et al. 2002; Chopin et al. 2001; Troell et al. 1999; Petrell and Alie 1996). The alternatives are land-based tank systems or ponds that can be separated from sea water inflow at periods of toxic algal blooms or oil spills, etc. In these systems, fish farm effluents are redirected through a series of tanks containing complementing organisms. The Sea Or Marine Enterprises in Israel integrated gilthead seabream with *Ulva* or *Gracilaria*, with the algae serving as a feed for commercially valuable abalone (Neori et al. 2004). With abalone (*Haliotis midae*) and seaweeds alone, a partial recirculation of the culturing water is feasible (Robertson-Andersson et al. 2008).

To establish a managed small ecosystem, that is adapted to site and region and that in addition sustains stakeholders and environment, is a very complex task, impossible to be tackled by individual farmers. Therefore, Canada has launched a new network CIMTAN (2011). CIMTAN is directed to collect additional knowledge and intensify interdisciplinary as well as multi-institutional information exchange between the experts on aquaculture on both coasts of Canada. Research and development of IMTAs has been conducted in Canada since 2001. The joint goal is to establish an easily adaptable system of IMTA with a set of nutritionally interacting species that mimics the natural condition of a diverse ecosystem, thereby being less vulnerable to e.g., microbial infections or parasite infestation.

At the same time most/all of the systems components should be of commercial value supplementing each other in reaching an acceptable profit for stakeholders and environment. Between January 2010 and December 2014, about 250 people will be involved in 14 projects systematically investigating the various aspects of IMTA from nutrient plumes to microbial interactions, detritivores (such as polychaetes and echinoderms), bivalves, fish parasites, and seaweeds (including *Saccharina latissima,* formerly *Laminaria saccharina*, *Alaria esculenta*, *Palmaria palmata*, and *Ulva* spp.) to infrastructure components, ecosystem modeling, and social implications for coastal communities. With the insights gained it will be easier to promote a sustainable and vibrant aquaculture industry in Canada and probably other temperate regions of the world.

22.1.3.3 Offshore Aquaculture

Aquaculture is continuously expanding in coastal seas and ashore, comprising farming in marine and brackish water environments (FAO 2010a, b). However, coastal waters host a highly competitive group of uses such as commercial shipping, areas exclusively reserved for the navy, extraction or disposal of sand, oil exploration and exploitation, as well as pipelines, cables, wind farms, nature reserves, and other marine and coastal protected areas. Recreational activities and fisheries are additional interests that deserve attention. This massive utilization of marine areas leads to stakeholder conflicts (Buck et al. 2004; Langan et al. 2006; Rensel et al. 2006). Additionally, farming activities may also generate negative environmental impacts on coastal ecosystems at local up to regional scales (e.g., Buck and Krause 2012), thus leaving little room for further expansion of modern coastal aquaculture systems. Locating aquaculture activities further offshore appears as a viable option to avoid stakeholder conflicts and to reduce environmental impacts to the coast (Corbin 2007). The term “offshore” within the context of aquaculture was defined by Ryan (2005) and is based on the moving of farm installations from nearshore sheltered environments to more exposed environments, which are commonly described as “high energy environment”.

Following Troell et al. (2012) and North (1987) considerable controversy has emerged over the proper development of offshore aquaculture, and its actual advantages over existing nearshore aquaculture. In general, many of the challenges for offshore aquaculture engineering involve adaptations of farm installation designs and operation protocols to a variety of physical factors, such as currents and wave actions: The robustness of the aquaculture systems to withstand harsh oceanographic conditions is one challenge, while the difficulties in anchoring and/or submerging structures in deep water is another. Major shipping routes have to be considered as well as migration routes of marine mammals. Logistic difficulties of transport and the operation and maintenance of offshore platforms of any farming enterprise must be evaluated.

Due to the scarcity of space even in the open ocean island territories or countries with relatively short coastlines, the concept of “multiple use” needs to be addressed. Germany is an example where the plans for the massive expansion of wind farms in offshore areas of the North Sea triggered the idea of a combination of wind turbines with installations for extensive shellfish and seaweed aquaculture (Buck 2002, 2004). A combined design of fish cages in the foundation of the turbines in addition to the extractive components of IMTA systems was discussed (McVey and Buck 2008). Offshore wind farms provide an appropriately sized area for farming that is free of shipping traffic. At the same time the infrastructure for regular service support is readily available. Such sites provide an ideal opportunity for devising and implementing a multiple-use concept (Buck et al. 2004; Michler-Cieluch 2009).

Some experimental-scale operations have shown the feasibility of offshore macroalgal farming (for review, see e.g., Buck et al. 2008). The focus of those systems was placed upon the technical design needed to withstand hydrodynamic forces and investigations on cultivation techniques to avoid dislodgement of laminarians (Buck and Buchholz 2004, 2005). Ebeling, Griffin, and Buck (unpublished data) were the first to calculate the economic potential of a seaweed farm (*Saccharina latissima*) within a planned wind farm off the coast of Woods Hole (Massachusetts, USA) in Nantucket Sound and found it being beneficial on a large scale.

22.2 Socioeconomic Aspects

Traditionally, the academic community has tended to approach aquaculture primarily from technological and environmental perspectives (Marra 2005). However, it has been recognized that aquaculture increasingly generates direct socioeconomic benefits through the supply of highly nutritious foods and other commercially valuable products, providing jobs and creating incomes. For example, the FAO reports for the Philippines that seaweed farming is currently the largest and most productive form of livelihood among the coastal population of the Philippines. In 2004, more than 116,000 families consisting of more than one million individuals were farming more than 58,000 ha of seaweed (FAO 2005–2011c). Enough and affordable manpower to maintain the farms is an indispensable prerequisite. Personnel on all levels of skills are required. The benefits for the well-being of coastal communities are reflected in the finding of a recent case study on a South African IMTA farm of abalone and seaweed presented by Nobre et al. (2010). In this study, the impact of direct permanent employment within the South African aquaculture industry on local communities was exemplified: The selected communities were characterized by high unemployment (85.7%), with more than 50% of the labor force being unskilled and semiskilled. It could be shown that employment of a high number of unskilled and semiskilled personnel in the aquaculture sector had a large local impact in previously disadvantaged coastal communities, where any increase in employment is valuable (Nobre et al. 2010). This is particularly relevant where unemployment is not only an economic issue but also a sociopolitical concern.

Thus, in addition to its own economic contribution, aquaculture can also induce, as a spin-off, economic contribution to other sectors that supply materials to aquaculture or use aquaculture products as inputs (ICES 2011). The numbers of people engaged in other ancillary activities, such as processing, farm construction, manufacturing of processing equipment, packaging, marketing, and distribution can be substantial. Indeed, estimates indicate that, for each person employed in aquaculture production, about three other jobs can be produced in secondary activities. The total aquaculture sector, encompassing finfish, shellfish, and seaweed aquaculture, and those supplying services and goods to them, provides employment and livelihoods to a total of about 20 million people (compiled from FAO 2011c).

Despite these positive effects, decisions about aquaculture development are often based on incomplete information, particularly in relation to the socioeconomic dimensions. As a consequence, inadequate accounts for trade-offs associated with different development options are made. Therefore, there is a risk that anticipated and much needed socioeconomic benefits from aquaculture expansion may come at the expense of increased and possible unsustainable pressure on ecosystem goods and services (Naylor et al. 2000), ultimately jeopardizing people's food security and livelihoods.

In contrast to many finfish aquaculture enterprises, there are, however, encouraging experiences made with seaweed aquaculture. An example on the important role of seaweed cultivation for local livelihoods and sustainable development is the introduction of seaweed farming on Zanzibar, Tanzania in 1989. In that year, the seaweed *Eucheuma* was imported from the Philippines and successfully grown on the East Coast of Unguja Island. Today, more than 90% of the farmers are women, which have changed the life in the villages. Not only did the women gain independent economic power, but the number of children suffering from malnutrition has also decreased, which indicates that the health of their mothers has improved. As daily income is secured, children are able to attend schools regularly. Furthermore, seaweed farming has also reversed the trend of rural depopulation, since it fostered self-employment of the village youths (Msuya 1997, 2006; Msuya et al. 2007).

The question remains though, how negative effects on the environment and positive socioeconomic consequences from aquaculture development can be balanced. For instance, although methods of cultivation can be adapted and vary being equally successful, the careful choice of the farming site seems to be essential for any aquaculture success (Trono 1990; Buck and Buchholz 2005). Notwithstanding, the seascapes are increasingly managed for multiple functions and services in addition to provision of food, and this requires the integration of ecological and socioeconomic research, policy innovation, and public education (ICES 2011). The multiuse dilemma has driven many researchers, experts, and policy makers to try and address issues related to the sustainability of aquaculture development from disciplinary/sectoral perspectives. However, aquaculture development raises questions that cannot be addressed in isolation. If it is to bring about the expected benefits, such as in the case of the seaweed farmers on Zanzibar, seaweed farming must address the interactions and functioning within wider ecosystem, social, economic, and political contexts.

A critical question is how to best guide the development of aquaculture that has the potential to support a portfolio of sustainable livelihoods and assist in poverty alleviation and food security (ICES 2011). Broader systematic perspectives on aquaculture, such as the "Ecosystem Approach to Aquaculture" (Soto et al. 2008), may enable analysis of trade-offs and sustainability aspects, especially with respect to net benefits for poorer resource users. Furthermore, local knowledge generated through active bottom-up participation and the application of transparent decision-making processes are some of the building blocks behind improved coordination of all the sector's stakeholders. Strengthening of institutional capacity and resources (including human capacity), both at national and international levels, is needed to enable development of aquaculture for poverty reduction and improved human well-being.

22.3 Direct Seaweed Applications and Bioactive Compounds

22.3.1 Introduction

Following the twentieth International Seaweed Symposium in Ensenada, Mexico, in 2010, several quite encompassing reviews have lately been published comprising various potential uses of seaweeds as functional food, feed supplement, or manure and soil conditioner with biological or pharmaceutical activities. Adding some more the following paragraphs provide an overview of the currently available information in published literature guiding specific interests in seaweed applications to the great number of detailed references collated already.

22.3.2 Seaweed for Food and Medication

Seaweeds have been used as food and for medical purposes since the late Pleistocene as Dillehay et al. (2008) reported from an excavation site at Monte Verde in southern Chile. Nine species of marine algae were recovered, among them edible species (*Durvillaea antarctica*, *Porphyra columbina*, *Sarcothalia crispata*, and *Macrocystis pyrifera*) and two nonedible ones (in the genus *Gigartina* and *Sargassum*). Some are nowadays being used as medical plants by indigenous people of that area and may have served the same purpose 14,000 years ago.

To date the food sector is still the most important field of application for the various species of seaweeds farmed or collected from the wild. While direct consumption is most common in the Asia-Pacific region, algal hydrocolloids are used worldwide in a great variety of food items as emulsifying, gelling, or water retention agents (Indergaard and Østgaard 1991; Murata and Nakazoe 2001; Bartsch et al. 2008). 86,100 tons of hydrocolloids were traded in 2009 comprising

58% of carrageen, ~31% alginates, and ~11% agar (Bixler and Porse 2011). The demand particularly for carrageen could not be met lately mainly due to the increased demands of the Chinese hydrocolloid industry. Moreover, collective quantity does not always suffice, since species as well as geographical location and climate where the seaweeds are grown and the season of harvest determine the chemical characteristics of the hydrocolloids and their quality. Quality is also influenced by the extraction methodology (Bixler and Porse 2011).

Aware of the fact that there is a great variety of chemical compositions and therefore bioactive properties in the different species of seaweeds Løvstad Holdt and Kraan (2011) supply a wealth of current knowledge on bioactive compounds of the most important species in 21 tables comprising the various polysaccharides, proteins, peptides, and amino acids as well as lipids and fatty acids, pigments, vitamins, iodine, phenolic components, and undesirable substances like heavy metals: The vast range of biological activities they listed originated from in vitro investigations up to clinical studies. Most spectacular are the antibacterial and antiviral activities that may partly be responsible for the records on positive effects against tumors and HIV. Important beneficial effects for human health lie also in the reduction of blood cholesterol levels and anti-diabetes and anti-hypertension effects. In addition to direct pharmaceutical uses of algal ingredients, a high-tech medical use of alginate as part of a matrix that can carry protein drugs is being developed. It utilizes the mucoadhesive property of alginate helping to retain the drugs in the gastrointestinal tract for a longer period, thereby improving drug bioavailability and effectiveness in the intestine (George and Abraham 2006). While the list of beneficial effects of seaweeds and their ingredients on humans is long, the process of getting them authorized as food or medical items can be as well (Løvstad Holdt and Kraan 2011).

22.3.3 Seaweed in Agriculture and Animal Diets

The large amounts of minerals, trace elements, vitamins, and iodine among other components render seaweeds, particularly the brown ones, a valuable addition not only to food but also to livestock feed and soil fertilization (lit. in Bartsch et al. 2008; Craigie 2011). Some direct or indirect beneficial effects hold for plants as well as animals of very different classes. An example is antihelmintic properties of seaweed extracts that can help not only mammals but also plants like tomatoes which suffer from nematode infestations in their roots (Løvstad Holdt and Kraan 2011; Craigie 2011). While commercial seaweed extracts have been available for 60 years, only 1% of the current seaweed industrial production goes into agricultural use, even though according to Craigie (2011) “seaweed extracts can modify plant and animal responses at a fundamental level.” However, the appropriate utilization of seaweed meal or extracts in agriculture and as feed addition has to be experimentally secured in advance of extensive use. Craigie (2011) reviews the history of seaweed utilization and the development of extracts and the responses of the soil and crops to various applications, e.g., different concentrations of extracts that can decide between inhibition and promotion of germination and growth. Table 12 (in Craigie 2011) summarizes the bioactive properties reported for seaweed extracts in plants and animals. As for plants the choice of algal species and extract concerning its nature and proportion in the feed of the respective livestock has to be carefully tested to avoid detrimental effects and improve overall health and benefit reproduction (Craigie 2011). Addition of 4% *Sargassum* meal to the feed of shrimp cultures reduced cholesterol contents of their muscle tissue by 29%, quite desirable for shrimp grown for human consumption (Casas-Valdez et al. 2006). In the case of cattle there can even be an advantage elicited in the shelf life of steaks, since a short-term feed addition of 2% *Ascophyllum* meal (Tasco) prior to slaughter not only results in a better marbling of steaks but also retains the red color over a longer period. The latter is due to a higher proportion of oxymyoglobin compared to conventionally fed cattle (Braden et al. 2007).

Of the 10 larger and 17 smaller producers of commercial seaweed extracts for agriculture that Craigie mentions, only three are presently located in Asia, that is in China, even though Asia is producing >98% of all seaweeds. The indisputable benefits of seaweed utilization in plant and animal farming excite expectations toward a more extended production and use in the future.

22.3.4 Other Applications of Seaweeds

The phycocolloids agar, carrageen and alginates have long been used for their water binding and thickening properties: While agar is not only known as a neutrally flavored thickener of stews, sauces, desserts etc., it is also indispensable as a solid culture medium in medical bacteriology and microbiological research. Alginates from brown seaweeds are used in printing dyes and for better adsorptivity of textiles. They are together with other seaweed components valued ingredients of cosmetics. Extracts typically found in cosmetics are made from *Ulva lactuca, Ascophyllum nodosum, Laminaria longicruris, Saccharina latissima, Laminaria digitata, Alaria esculenta,* various *Porphyra species, Chondrus crispus*, and *Mastocarpus stellatus* (Cosmetic Ingredient Dictionary 2002–2011).

The latest innovation is a textile fiber named SeaCell®. It is a cellulose-based fiber produced from seaweeds like *Ascophyllum nodosum* and used as a yarn for clothing or for filling duvets (Smartfiber 2010).

Another field of high interest and great demand is the partial replacement of fish meal by seaweeds. Only a small selection of seaweed species will probably be suited. Experiments by Walker et al. (2009) showed positive results with up to 30% *Porphyra* spp. in the diet of juvenile Atlantic cod. If *Porphyra* ("nori") was introduced into the commercial aquaculture of fish, demand and price of the already valuable seaweed would probably rise enormously.

Due to their high carbohydrate content seaweeds can be fermented to methane (biogas) and in many places (mainly beach cast) seaweeds are considered a potential CO_2-neutral and renewable energy supply (lit. in Bartsch et al. 2008; Roesijadi et al. 2008; Chung et al. 2011).

Bioremediation of eutrophic waters has been mentioned above in relation to aquaculture. It would also work for waters supplied with an excess of nutrients from other sources. If the resulting quantity of algal biomass was not good enough to be introduced into a high quality production line, it may still serve as a good feedstock for biofuels.

22.4 Conclusion

Seaweeds have accompanied human history for about 14,000 years. Seaweed research from simple observation to organized experiments has helped to install an extensive aquaculture industry that produced close to 14.8 million tons in 2009, while it was just a few kg in the 1950s. Large and many small enterprises worldwide secure thousands of family incomes and are therefore of high socioeconomic importance. The global "hot spot" of seaweed farming as well as direct use of these macroalgae as food items is Asia. Algal ingredients like the phycocolloids agar, alginate, and carrageenan are in demand by the food industry, medical, and technical applications. The use of seaweed meal or extracts for agricultural applications bears a great potential for expansion. To satisfy the market demand not only for seaweeds but also highly requested protein sources like finfish, shellfish, and crustacea, the relocation of culturing sites to offshore areas is suggested for wind farms at sea as a multiuse concept. Another promising and intensively developing field of aquaculture is the expansion of Integrated Multi-Trophic Aquaculture (IMTA) systems where commercially valuable organisms from different trophic levels, some fed and some extractive, are combined in a culturing system, ideally sustaining each other and with the help of seaweeds even bioremedial for the environment.

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Erratum to: Cold-Temperate Seaweed Communities of the Southern Hemisphere

Pirjo Huovinen and Iván Gómez

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Fig. 14.3: The bold line indicating the distribution of *Macrocystis* in South Africa should not be in black, but in red.

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