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Seaweed Biology

Novel Insights into Ecophysiology, Ecology and Utilization

Bearbeitet von
Christian Wiencke, Kai Bischof

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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