Chapter 1
Antarctic Seaweeds: Biogeography, Adaptation, and Ecosystem Services

Iván Gómez and Pirjo Huovinen

Abstract Seaweeds (macroalgae) represent the most striking benthic organisms in the Antarctic near-shore ecosystems. Their abundance, relevant roles as primary producers, and foundation organisms were recognized since the first Antarctic explorations. Furthermore, especially since the 1960s, improvements in the sub-aquatic survey techniques and laboratory facilities expanded considerably our knowledge on ecology, reproduction, and environmental adaptation of seaweeds whose biological processes determine much of the biogeochemical cycles in the Antarctic coastal systems. In recent years, the imminence of the climate change and the direct impact of human activities, which are affecting vast regions of the Antarctica, have highlighted the importance of seaweeds as central components shaping the structure, functions, and supporting services of benthic ecosystems under changing polar environment. The present book is aimed to put together the knowledge and experience gained in recent years by diverse research groups. Many of these research efforts have long tradition, while others have brought more recently important new approaches in the study of these organisms with benefits for the whole polar science. We believe that this initiative is timely and urgently needed in order to improve our scientific knowledge on these fascinating organisms. In this chapter, we describe the book's framework, summarizing the most important advances in areas related with diversity, biogeography, ecophysiology, biological interactions, and chemical ecology of Antarctic seaweeds. Finally, considerations regarding the major gaps and challenges as well as the new directions in the study of Antarctic seaweeds are outlined.

Keywords Antarctic · Climate change · Antarctic marine flora · Ecosystem functions

I. Gómez (✉) · P. Huovinen
Instituto de Ciencias Marinas y Limnológicas, Facultad de Ciencias,
Universidad Austral de Chile, Valdivia, Chile

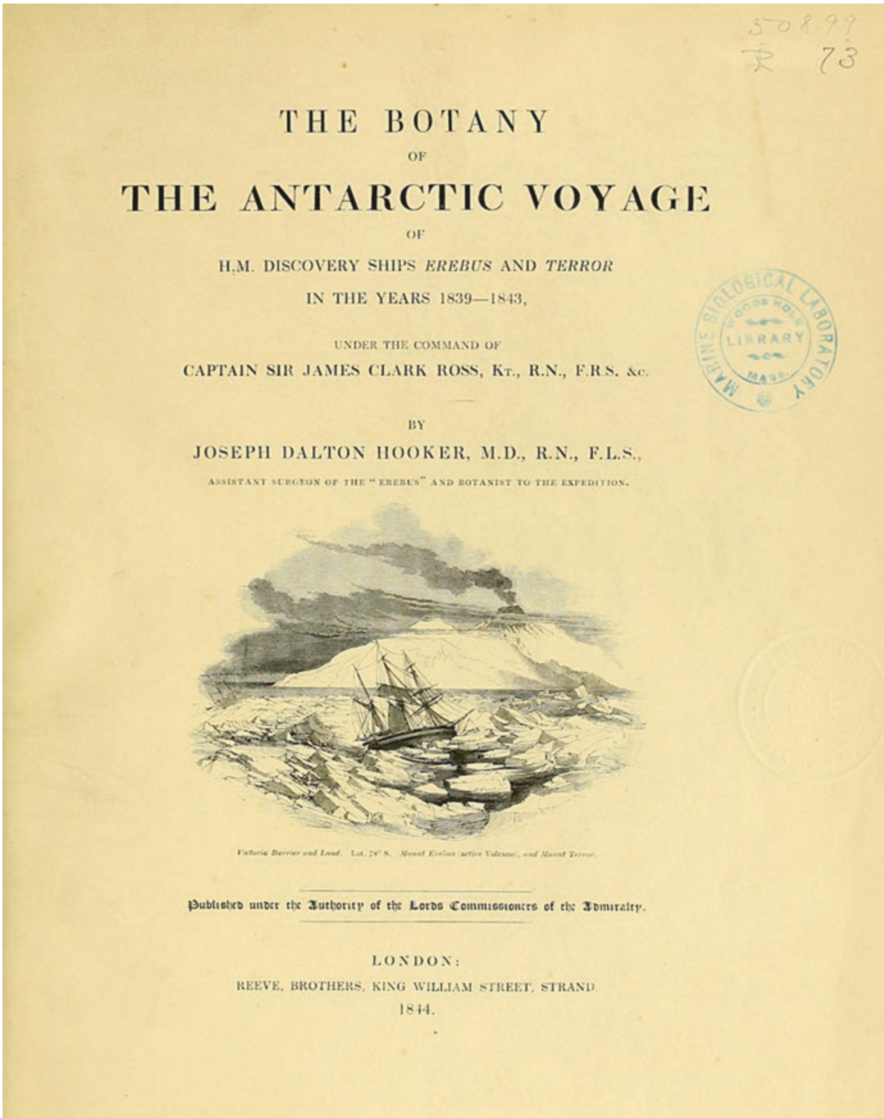
Research Center Dynamics of High Latitude Marine Ecosystems, (IDEAL), Valdivia, Chile
e-mail: igomezo@uach.cl; pirjo.huovinen@uach.cl

I. Gómez, P. Huovinen (eds.), *Antarctic Seaweeds*,
https://doi.org/10.1007/978-3-030-39448-6_1

1.1 Introduction: The Historical Context

In recent decades, important advances have been demonstrated in different areas of knowledge on Antarctic seaweeds, from organisms to ecosystems. However, in order to understand the roles and services of seaweed communities in Antarctica currently marked by climate change, it is essential to go back to the history of this endeavor. The first explorations of Antarctic seaweeds in the nineteenth century (Gaudichaud 1826; Hooker 1847) had already documented the exuberant presence of benthic seaweeds and recognized their importance for the coastal ecosystems in the Antarctic, especially around the Antarctic Peninsula. In his book *The Botany of the Antarctic Voyage of H.M. discovery ships "Erebus" and "Terror" in the years 1839–1843, under the command of Captain Sir James Clark Ross* (Fig. 1.1), one of most complete records of marine and terrestrial flora of the Southern Ocean, the British botanist Joseph D. Hooker disclosed much of the extraordinary conditions that characterize the habitat of many Antarctic seaweeds. Later, another important researcher, Karl Skottsberg, expanded this information from different Antarctic expeditions in the early twentieth century (e.g., Skottsberg 1907). During the 1960s and 1970s, descriptions based on scuba diving surveys carried out by Neushul (1965), Delépine et al. (1966), Zaneveld (1966), and Lamb and Zimmermann (1977), among others, confirmed this, highlighting the dominance of large endemic Desmarestiales at depths >10 m, where they occupy similar role as kelps as the dominant seaweed group in the Northern Hemisphere and the Arctic. The unique characteristics of the Antarctic marine flora reflect the complex biogeographic and evolutionary processes that followed the formation of the Antarctic Circumpolar Current (ACC) around 30–35 Ma and consequent full glaciation of the Antarctica (Clayton 1994). Diverse surveys across different sites in the Antarctic, including communities growing under ice shelves, expanded considerably our knowledge on vertical distribution, biomass, and diversity of seaweeds (Zielinski 1981, 1990; Amsler et al. 1995; Klöser et al. 1993, 1996; Brouwer et al. 1995).

Due to the harsh climatic conditions and logistic restrictions in Antarctica, advances in our knowledge on reproduction, phenology, and acclimation to the polar environment were only possible since the 1980s. Using cultured material, Moe and Henry (1982) described for the first time various aspects of the development of early phases of *Ascoseira mirabilis.* The first studies unraveling the seasonal development, life history, and physiological performance of Antarctic seaweeds were based on algae grown under cultivation conditions simulating the Antarctic light regime (Wiencke 1990). Based on these findings, two main growth strategies were defined: the season responders start growth and reproduction when environmental conditions are optimal in spring and summer, while the season anticipators develop during late winter and spring. Thereafter, the number of investigations focused on physiology of photosynthesis, growth, chemical ecology, etc., increased (revised in Wiencke 1996). A noticeable finding was that various endemic Antarctic brown algae, such as *Ascoseira mirabilis*, *Cystosphaera jacquinotii*, *Desmarestia anceps*, and *Himantothallus grandifolius*, exhibit thallus anatomical



THE BOTANY

OF

THE ANTARCTIC VOYAGE

OF

H.M. DISCOVERY SHIPS *EREBUS* AND *TERROR*

IN THE YEARS 1839—1843,

UNDER THE COMMAND OF

CAPTAIN SIR JAMES CLARK ROSS, KT., R.N., F.R.S. &c.

BY

JOSEPH DALTON HOOKER, M.D., R.N., F.L.S.,

ASSISTANT SURGEON OF THE "EREBUS" AND BOTANIST TO THE EXPEDITION.

Victoria Barrier and Land. Lat. 78° S. Mount Erebus (active Volcano), and Mount Terror.

Published under the Authority of the Lords Commissioners of the Admiralty.

LONDON:

REEVE, BROTHERS, KING WILLIAM STREET, STRAND.

1844.

Fig. 1.1 Cover page of Hooker's publication describing the flora of the Southern Oceans

and functional characteristics resembling those of large kelps from the Northern Hemisphere (Drew and Hastings 1992; Gómez et al. 1995; Fig. 1.2). Here, the most remarkable morpho-functional adaptations of large Antarctic brown algae are their very low light demands for growth and photosynthesis and an efficient operation of light-independent carbon fixation (LICF) at the meristematic zones, which allow these organisms to display positive carbon balance at depth close to 30 m (Gómez et al. 1997). The knowledge on these structural and functional aspects of

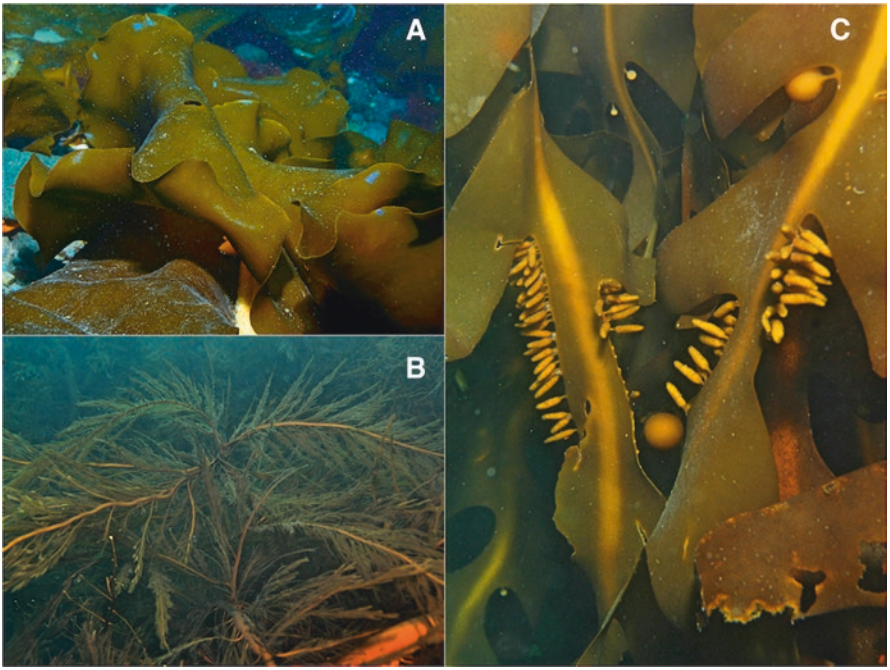


Fig. 1.2 Large endemic brown algae are the most representative components of the Antarctic costal systems. (**a**) *Himantothallus grandifolius*, (**b**) *Desmarestia anceps*, (**c**) *Cystosphaera jacquinotii.* (Photos by Ignacio Garrido)

photosynthetic responses had important implications for understanding the biological interactions between seaweeds and their associated biota (Zacher et al. 2007; Iken et al. 2009; Amsler et al. 2011).

In the last decades, the Antarctic ozone depletion and associated increase in UV-B radiation, as well as the environmental shifts driven by climate change, oriented the research of Antarctic seaweeds. In this context, various studies have examined the effects of changing irradiance on different algal assemblages across Antarctica (Schwarz et al. 2003; Zacher et al. 2007; Huovinen and Gómez 2013; Clark et al. 2017; Deregibus et al. 2016). At an ecosystem level, seaweeds have been commonly recognized as important sentinels of climatic change in the Antarctic, highlighting the remarkable capacity of these organisms to adapt to new habitats (Quartino et al. 2013), and also providing some key ecological ecosystem properties that permit the maintenance of species richness and biomass (Valdivia et al. 2015). Through their ecosystem engineering functions, especially large endemic brown algae are able to minimize environmental variability enhancing the resilience of the whole system (Ortiz et al. 2017).

Despite these advances, much of the predictions related with adaptation and fate of Antarctic seaweeds are limited by scarce molecular evidence. From this perspective, the findings of an increasing number of cryptic species with Antarctic/sub-

Antarctic or even more vast joint distribution (van Oppen et al. 1993; Hommersand et al. 2009; Billard et al. 2015) challenge some traditional concepts related with the evolution and biogeographic patterns of the Antarctic marine flora (Crame 1992; Clayton 1994). According to current predictions, climatic anomalies, e.g., enhanced temperature, increased storms, and winds, will be able to break the ecological isolation of Antarctica and facilitate the arrival of temperate species (Fraser et al. 2018), with impacts on diversity and genetic configuration of local communities yet not well understood.

1.2 Antarctic Seaweeds in the Wake of Climate Change

The climate, oceanography, and related ecosystem processes in Antarctica and its surrounding oceanic system have been changing rapidly in the last decades (reviewed in Constable et al. 2014). Accelerated regional warming was reported especially in the WAP region almost 20 years ago (Vaughan et al. 2003). According to the IPCC scenarios, the mean annual air temperature in this region was predicted to increase by 1.4–5.8°C until 2100 (Clarke et al. 2007), although strong natural variability seems characteristic in this region (Turner et al. 2016). The surface waters of the Bellingshausen Sea have warmed by 1°C in summer since the 1950s (Meredith and King 2005), while Schloss et al. (2012) reported an increase of more than 2°C in winter sea surface temperature between 1991 and 2006 in Potter Cove (King George Island). This tendency and the possible effects on the polar system were recently highlighted in the last IPCC report (IPCC 2019). As a synthesis the report indicates that the Southern Ocean (area corresponding to 25% of world's oceans) has been warming at alarming rates, being responsible for 45–62% of the global ocean warming during the period 2005–2017. Although no clear overall trends in Antarctic sea ice cover were evident for the period 1979–2018, a strong decline has been observed recently (2016–2018), which can pose threats to the photosynthetic organisms due to unpredictable changes in the light regime (see Chap. 7 by Huovinen and Gómez). In the Arctic, massive ice-sheet losses, exceeding the rates of modeled estimations, have been observed (Bronselaer et al. 2018). Here, the role of albedo-reducing light-absorbing impurities in ice and snow fields exacerbating ice loss has been emphasized (Benning et al. 2014; Tedesco et al. 2016; Tedstone et al. 2017). Dark snow phenomenon has recently also been associated with decreased albedo in Maritime Antarctic (Huovinen et al. 2018). Recently, the active role of ice sheets and icebergs in the global carbon cycle has been recognized (reviewed by Barnes et al. 2018; Wadham et al. 2019) and can have important consequences for the adjacent marine realm in areas like Maritime Antarctic (Hood et al. 2015). Although various impacts of these changes are broadcasted for pelagic realms, their implications for the processes occurring in the Antarctic shallow benthos are much less known (Barnes and Conlan 2012; Constable et al. 2014).

The increasing number of volumes devoted to the present and projected impacts of global climate changes on the Southern Ocean and their different ecosystems (e.g., Bargagli 2005; Bergstrom et al. 2006; Rogers et al. 2012; Tin et al. 2014; Kanao et al. 2018) is a clear evidence of the importance of understanding their global consequences. Antarctica can be regarded as a natural laboratory where its physical environment brings the adaptation capacities of organisms to an extreme limit. In this context, seaweeds, as fundamental components of the Antarctic coastal systems, can give important insights into the structure and functioning of the biota in the new scenarios driven by climate change.

1.3 The Book

Based on recent quantitative, observational, and experimental evidences, this book updates the state of art about the diversity and geographic distribution of seaweeds as well as their biological interactions and responses to the environment, which is fundamental for understanding the coastal processes in a changing Antarctica. The main themes and the overall scientific framework discussed in the book can be summarized in Fig. 1.3.

1.3.1 Diversity and Biogeography

Compared to other biogeographical regions in the Southern Hemisphere, e.g., southern Australia, New Zealand, and the southern Chilean coast, the diversity of seaweeds in the Antarctic has been traditionally considered low. Based on Wiencke and Amsler (2014), the number of species is 124, showing high endemism (35%). In their chapter (Chap. 2), Oliveira et al. indicate that the richness of Antarctic seaweeds has been underestimated. Based on previous information and recent molecular surveys, the authors report a diversity of 151 species of which 85 are Rhodophyta, 32 Chlorophyta, and 34 Ochrophyta (most of them brown algae). Likewise, this update decreased the percentage of endemism to 24%. Overall, the increase in the number of catalogued species can be explained by improvements in the identification tools, e.g., the use of DNA barcoding, more complete gene databases, and more efficient approaches to detect, e.g., cryptic species. However, a conclusive outcome of this diversity is far from definitive: a lack of baseline datasets in order to accurately detect local loss of native species, or their replacement by alien assemblages, still persists. Thus, extending the geographical range and number of surveys, adjusting better the inventories of phylogenetic markers, and deepening the examination of less conspicuous algal groups, such as crustose and endophyte species, a hidden diversity normally overlooked, are suggested.

The Antarctic Circumpolar Current has defined the structure, diversity, and functioning of the biomes of the Southern Ocean. Fraser et al. (Chap. 3) make a comprehensive analysis of environmental and oceanographic conditions that characterize Antarctic from the sub-Antarctic regions, the dual role of ACC acting as an efficient

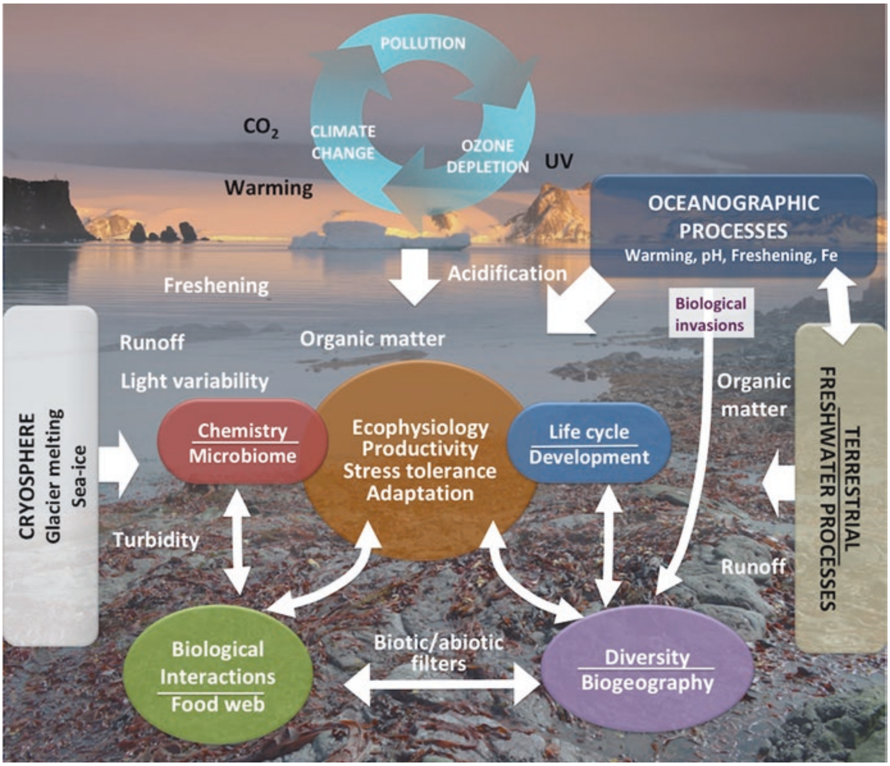


Fig. 1.3 Schematic presentation of the major drivers, organismal processes, and biological interactions of Antarctic seaweeds. The framework is based on the conclusions of the different chapters in this book

barrier and also as a bridge connecting marine assemblages and the requisites of organisms permitting their dispersal across these environmental gradients. Rafting of floating seaweeds driven by prevailing winds across the different fronts in the Southern Ocean appears as a central mechanism promoting transoceanic connections, not only of seaweeds but also invertebrates. The definitive establishment and persistence of new taxa in these zones will depend on different environmental filters, e.g., physical and biological constraints, and also on various organismal features related with reproductive viability, physiological capacities, etc.

Probably the extent of exchange of species and hence genetic fluxes between sub-Antarctic and Antarctic regions lie in the diversity of taxa that can be transported across long distances and their ability to remain alive during their journey. Macaya et al. (Chap. 4) indicate that a total of 39 species (3 Chlorophyta, 14 Ochrophyta, and 22 Rhodophyta) have been reported drifting, stranded or floating in Antarctica or crossing the Antarctic Polar Front (APF). Considering that many cold and cold-temperate species at both sides of the ACC show remarkable physiological adaptions to biotic and abiotic factors, e.g., grazing, UV radiation, and temperature, they could be able to arrive and colonize different locations around the Southern Ocean. An example is the floating large brown algae commonly used by different hitchhiking biota (e.g., barnacles, amphipods, algae). Interestingly, the authors suggest that various Antarctic seaweeds, some with floating or buoyancy capacity, have the physiological potential to travel out of the Antarctic.

In their chapter (Chap. 5), Pellizari et al. indicate that the diversity and biogeographic patterns of Antarctic seaweeds have begun to change. Here, the changing environmental scenarios in the Southern Ocean, related mostly with circulation and warming, will determine the new seaweed diversity. Using the seaweed assemblages of Deception Island in the South Shetlands as a case study, the authors describe an important presence of species with broad geographical distribution, especially Chlorophyceans, indicative of recent arrival. Apparently, areas like this characterized by peculiar physicochemical conditions could become key places to study the new Antarctic biodiversity, its biogeographic divergences and connections.

The Antarctic continental margins or peri-Antarctic islands are zones that evidence the long evolutionary history of seaweeds within the Southern Ocean. Guillemin et al. (Chap. 6) analyzed the sequences of mitochondrial and chloroplast markers in eight Antarctic species of green, brown, and red seaweeds in order to determine the genetic patterns in the context of the quaternary climatic oscillations (QCO). The haplotype network revealed that the studied Antarctic seaweeds show very low genetic diversity, and significant signatures are indicative of a recent population expansion after a massive constriction during the Last Glacial Maximum (20 Ka). Thus, the authors agree with a theory that this marine flora survived *in situ* in a unique refugium and subsequently recolonized the multiple postglacial open areas using the ACC as a predominant driving force.

In all, Antarctica is not a physically isolated continent, and in a scenario of increasing warming, the influx of marine organisms arriving, e.g., via rafting to its coasts, can find new opportunities for colonization, which finally will modify the local diversity (Fig. 1.3). Here, the examination of large-scale patterns of seaweeds may provide clues to evaluate aspects of endemism, biological corridors, and expansion of geographical distribution of various algal species. In this context, an account of the genetic footprints of past diversity can help to understand not only the large-scale processes that occurred along the evolution of the Antarctic flora, but also its future genetic structure.

1.3.2 Environment and Ecophysiology

Due to the harsh environmental conditions, the Antarctic has commonly been regarded as an inhospitable place for living organisms. Antarctic biota has adapted to these conditions and thrives in different types of habitats, some marked by extreme physical variability. However, the new environmental features as a consequence of regional warming and related phenomena occurring in the cryospheric realm, as well as direct anthropogenic pressures, are challenging the adaptive strategies of seaweeds in manners still not well understood.

Light is probably the most important environmental factor determining the phenology, spatial distribution, and productivity of Antarctic seaweeds. In Chap. 7, Huovinen and Gómez describe the underwater optics in the context of present and future variability and its importance for seaweed photobiology. The optical properties of the coastal waters, including their light absorbing and scattering components, define the underwater light environment at ecologically relevant depths (down to 40 m). Despite Antarctic seaweeds being regarded as shade-adapted organisms, they also show a striking capacity to acclimate to sudden increases in solar radiation. However, the natural variability in light regimes is being altered due to earlier sea ice breakup, enhanced runoff from the terrestrial and glacial melting, enhanced UV-B levels as a result of ozone depletion, etc. These new scenarios are accompanied by emergent stressors (e.g., local freshening, acidification, increasing contaminant load) whose influence on the underwater light climate in the Antarctic up to now is not well understood.

Probably one of the most striking signals of warming in the Antarctic is the retreat of glaciers, which is creating new ice-free habitats for benthic organisms. The question of how the future coastal scenarios driven by climate change will affect the colonization and fate of seaweeds was addressed by Quartino et al. (Chap. 8). In fact, the increased seaweed biomass will enhance the carbon flux and hence the organic matter towards the higher trophic levels. Due to some species attaining biomass values close to 10 kg m^{-2} wet weight, a strong impact on the coastal productivity can be expected. However, in these highly dynamic new habitats, reflected in the model system of Potter Cove in King George Island, seaweed colonization follows the sharp gradients set by the light penetration, which are strongly modified by enhanced sedimentation. Considering their great abundance and functional role as ecosystem engineers, benthic seaweeds can become important carbon sink in these systems. For instance, it has been estimated that seaweeds can account for a global net primary production of ca. 1.5 Tg C yr^{-1} (Krause-Jensen and Duarte 2016), thus forming part of the "blue carbon" components.

Low water transparency in the new ice-free areas affects the physiological performance of seaweeds in different ways. Deregibus et al. (Chap. 9), based on long-term records in areas nearby a retreating glacier at Potter Cove, describe the photosynthetic carbon balance of seaweeds (the gain of C in photosynthesis versus that lost in respiration) and its changes in relation with the light climate. Considering light requirements and photosynthetic efficiency estimated from P-E curves, the authors indicate that vertical distribution limits of some seaweed species changed as a result of enhanced turbidity. Accuracy of the carbon balance estimations requires a robust temporal set of solar irradiance data; thus, the importance of permanent *in situ* monitoring accounting for variations at short (hours, days) and long (monthly, inter-annual) timescale was highlighted.

The performance of seaweed populations under changing environmental regimes depends on the survivorship of their early reproductive stages. However, life cycle stages (e.g., spores, microscopic gametophytes, embryonic sporophytes, etc.) can be highly sensitive to environmental stressors. In Chap. 10, Navarro et al. make a thorough review of the aspects of the physiology of propagules of Antarctic seaweeds and how they respond to major physical factors, e.g., solar radiation, and temperature, considering present and future settings. UV effects are in many cases modified by temperature, showing interactions of factors. The response mechanisms and degree of tolerance of early developmental stages mirror those observed in the parental individuals. For example, differential responses to UV radiation determined in adult populations of congeneric and conspecific species from distinct depth zones (e.g., subtidal versus intertidal) or geographical origin (e.g., Antarctic versus sub-Antarctic) have also been observed in their propagules.

Antarctic seaweeds can be very abundant in terms of biomass and account by more than 50% of the coastal primary productivity, especially around the Antarctic Peninsula. Much of this ubiquity is strongly linked with efficient morpho-functional adaptations that have permitted these organisms to occupy niches characterized by sharp physical gradients. In Chap. 11, Gómez and Huovinen discuss the importance of the form and function of seaweeds. In general, the functional forms are well distributed along the major groups of Antarctic seaweeds: coarsely branched and leathery species, which can be regarded as the most robust and large-sized forms, represent 49% of the total number of species. In this group, endemic brown and red algae dominate, mainly growing at the subtidal zone. Filamentous, finely branched and foliose species (41%) belong mostly to green and red algae, common at shallow and intertidal sites, and are geographically widely distributed. Each of these morphs are integrated in different life strategies and hence distinct ecosystem functions. For example, perennial canopy-forming species show competitive abilities for light and substrate, but in general prevail less in sites subject to strong physical perturbation. Here, small colonizers and opportunistic species dominate in virtue of rapid metabolic adjustments and turnover rates.

The different chapters reveal that the abiotic environment of Antarctica is changing in extent that is already affecting several aspects of the physiology of marine biota in general and seaweeds in particular. The emergence of new habitats available as the glaciers retreat is modifying the composition, structure, and trophic relations of the benthic communities dominated by seaweeds. Apparently, a strategic factor underlying these responses is the ability of adult plants and their propagules to acclimate, via different functional traits, to the environmental shifts.

1.3.3 Ecological Functions

The ecological succession in Antarctic benthos determines the structure of the mature community and its biological network. Different types of positive and negative interactions between algal assemblages, invertebrates, fish, and microorganisms can be identified as the community develops. Based on *in situ* experiments, Campana et al. (Chap. 12) describe the successional stages and their biotic interrelations in a coastal site near Potter Cove. During the first three months, the incipient community is dominated by microorganisms and benthic diatoms, which apparently promote the development of small ephemeral filamentous green algae. The assemblage is successively enriched by the presence of various foliose and crustose forms of red algae and during late algal succession (after 4 years) by some perennial species of *Desmarestia*. The different components of the succession respond differently to environmental factors such as UV radiation, grazing, glacier retreat, and sea ice, and hence the structure and the biotic relations change dynamically within this early community.

Grazing is probably the most important biotic factor controlling the structure and composition of seaweed-dominated communities. In Antarctic benthic systems, the early successional stages dominated by small-sized seaweeds and periphyton represent excellent models to study how grazing modifies different ecological properties not only of native assemblages but also of alien species, whose arrival and establishment will be stimulated by climate warming. In Chap. 13, Valdivia determined by means of mathematical simulations the impact of mesograzers in sub-Antarctic and Antarctic sites connected by dispersal. *Ulva* sp. was regarded an alien species, being highly competitive in the Antarctic but not in the sub-Antarctic littoral. The results indicated that Antarctic mesograzers have a deterministic and marked effect on the biomass of the alien seaweeds; however, projected climate-change-driven shifts in temperature or pH could decrease the potential of, for example, amphipod grazers to control the development of invaders.

Antarctic seaweeds harbor complex and intricate microbiomes, which exert important influence on different molecular and biochemical processes of the algal host. Hitherto much of the coevolutionary processes of this association have been little studied. However, it is reasonable to argue that microbiota plays important functional roles in the ecology of Antarctic seaweeds. Gaitan-Spitia and Schmid (Chap. 14) review various aspects of structure, diversity, and functioning of Antarctic microbiomes and their implications for seaweeds. Members of phylum Actinobacteria show high diversity and persistence among different seaweed species, while Firmicutes are less represented. In general, the microbiomes associated to seaweeds are different from those found in the surrounding environment, which suggest that the bacterial composition is regulated by the seaweed host. Apparently, this feature reflects adaptive strategies to respond to multiple environmental conditions, e.g., antioxidation, antimicrobial activity, photoprotection, etc.

Seaweeds and microphytobenthos represent the basis of the Antarctic coastal food web. Because coastal areas can become highly perturbed, the dynamics and stability of the interspecific interrelations have fundamental influence on the whole benthic ecosystem at different spatial and temporal scales. Momo et al. (Chap. 15) determined that the food web at Potter Cove is based on 24 seaweed species and diverse other photosynthetic organisms, such as epiphytic and benthic diatoms and phytoplankton as well as their detritus. The system is also hyperconnected indicating multiple energy pathways. Considering extinction thresholds, this network can be regarded as relatively resilient to local losses of seaweed species. Similarly, using as a model Fildes Bay, a coastal system geographically close to Potter Cove, Ortiz et al. (Chap. 16) analyzed different keystone species complexes, which contribute importantly to the emergent network properties, such as growth, organization, development, maturity, and health of the ecosystem. The theoretical framework (based on network analysis, *ascendency*, and *loop analysis*) identified detritus, the phyto-zooplankton complex, sea stars, sea urchins, and seaweeds as the major components determining the overall structure and function of this system. Similar to Potter Cove, Fildes Bay appears to be a less developed system compared to other cold-temperate system, but being highly resilient to physical perturbations.

The described examples on the ecology of the coastal system in the Maritime Antarctic reveal complex biological interactions between, e.g., algae, microbiota, invertebrates, and fish, which are strongly regulated by the physical environment. In this scenario, seaweeds are identified as key components from the early stages of succession to the consolidate communities. Due to the strong influence of physical factors from terrestrial, freshwater, cryospheric and atmospheric processes, the structure, function, and trophic interrelations in these communities are in general very resistant to disturbances (Fig. 1.3). Thus, it seems that there are internal mechanisms operating at individual (e.g., efficient growth strategies, multiple anti-stress mechanisms) as well as at population and community (e.g., filters controlling native and alien species, high biological complexity based on species and biomass richness) levels, providing the system with a high resilience.

1.3.4 Chemical Ecology

The trophic relations in the Antarctic benthic system show a balance between consumption by herbivores and their deterrence. Amsler et al. (Chap. 17) review the recent advances in relationship between seaweeds and, e.g., amphipods, gastropods, and fish. Diverse halogenated monoterpenes and phlorotannins (phenolic compounds found in brown algae), and probably various other compounds, confer many species of Antarctic seaweeds unpalatability to different kinds of herbivores. Interestingly, the relationship between some seaweeds and various species of amphipods includes mutualism, in which chemically defended algae offer protection from, e.g., omnivorous fish, while amphipods reduce the biofouling and epiphytic load of the thalli.

Chemical defenses based on phlorotannins operate not only against grazing, but also form part of a wide suite of constitutive anti-stress mechanisms. In Chap. 18, Gómez and Huovinen summarize the different aspects that determine the synthesis and accumulation of these substances, which in some Antarctic brown algae can represent up to 12% of the dry weight. These compounds have different functions as grazing deterrents, reactive oxygen species (ROS) scavenging agents, and metal chelators and can be allocated in different thallus parts to optimize defense. Although phlorotannins are regarded as UV screening substances, no evidence on UV induction in Antarctic seaweeds has been reported. However, the antioxidant capacity increases substantially along with increasing phlorotannin concentrations in algal extracts, even in algae not naturally exposed to UV radiation.

The high prevalence of chemical defenses observed in Antarctic seaweeds is remarkable and suggests their central role in defining their dominance and biological interactions in the Antarctic coastal ecosystems (Fig. 1.3). Particularly, the constitutively high levels of phlorotannins measured in various dominant brown algae (e.g., *Desmarestia anceps*, *Himantothallus grandifolius*) open interesting questions about the activation of anti-stress mechanisms based on chemical substances with multiple primary and secondary functions. For seaweed assemblages subjected to climate-change-driven environmental shifts, such defenses could confer ecological advantages.

1.4 Gaps, Emerging Challenges, and Future Directions

The different chapters throughout this book update the current knowledge and provide novel insight into various aspects on diversity, ecophysiology, and ecology of Antarctic seaweeds, with particular emphasis on their responses to the changing polar environment. However, several gaps still persist and new questions require attention in the near future.

- *Long-term assessment:* Due to logistical constraints, research in Antarctica is normally restricted to the spring-summer season. This time frame clearly does not permit covering the entire environmental variability to which Antarctic organisms, especially annual and perennial species, are exposed. For example, many gaps exist on the metabolic performance of seaweeds (e.g., carbon and nutrient metabolism, use and remobilization of photoassimilates, etc.) during the long Antarctic winter. In fact, the few studies addressing photosynthesis in winter or under ice cover suggest that seaweeds are at their physiological limit during this period (Gutkowski and Maleszewski 1989; Drew and Hastings 1992; Schwarz et al. 2003). These studies should be complemented with long-term monitoring of annual and inter-annual physical fluctuations in order to delimit the ranges of acclimation and adaptation of organisms. Because most of the monitoring platforms deployed around the Antarctica are designed to record changes in the open ocean, long-term or real-time baseline information of near coastal processes is still very limited. In this context, the long-term observations focused on the impact of the retreating Fourcade Glacier in Potter Cove (King George Island) represent an important effort in gaining insights into the responses of benthos at ecological scales (Meredith et al. 2018; see Chap. 8 by Quartino et al. and Chap. 9 by Deregibus et al. and references therein).
- *Molecular ecology*: Although remarkable improvements in biomolecular tools have considerably expanded our capacities to record and elucidate the taxonomical status of Antarctic species (Held 2014), many seaweeds are still not well classified, are cryptic or due to their life form (e.g., epiphytes, endophytes or prostrates) remain undiscovered. Another important limitation challenging the efforts to expand not only the genetic inventories, but also the general knowledge

on Antarctic organisms, is that the surveyed areas are strongly biased towards some regions, especially around the Antarctic Peninsula and in sites in direct proximity to research stations, while other coasts, e.g., from the East Antarctic, have been scarcely visited (Mormède et al. 2014). Thus, it is assumed that in the near future, along with the advances in phylogeography and population genetics as well as in geographic coverage, the number of Antarctic seaweed species, both native and recently arrived, will increase (see Chap. 2 by Oliveira et al.).

There a considerable lags in our understanding of gene expression and regulation. This is probably one of the weakest areas in the study of seaweeds in general and Antarctic species in particular. Thus, use of molecular tools such as transcriptomic analysis will help identify the metabolic pathways and adaptive strategies that Antarctic seaweeds exhibit beyond their tolerance threshold. For example, recently high and constitutive gene expression of various physiological reactions, including photochemical and inorganic carbon utilization components, from RNA-Seq analysis was reported for the first time for an Antarctic endemic species (the brown alga *Desmarestia anceps*; Iñiguez et al. 2017). Clearly this type of techniques open new avenues for the identification of transcripts that are differentially expressed under different stress conditions. On the other hand, the new molecular tools together with improved physiological methodologies are fundamental to predict whether key Antarctic seaweeds exhibit the molecular machinery to respond to ongoing and near-future impacts of climate change.

- *Ontogenetic development and life cycle responses*: Developmental phases (e.g., spores, gametes, and embryonic sporophytes) are highly sensitive to environmental changes (reviewed in Chap. 10 by Navarro et al.). However, they are often overlooked due to their small size or because the logistical constraints associated with their isolation, culture, and experimentation in Antarctica (Wiencke 1988). Considering that the fate of these cells determine the structure and dynamics of further life phases, it is urgent to conduct research focused on the acquisition of stress tolerance capacity at different developmental stages and how this resilience is "transferred" over generations. Following important developments in the identification and visualization techniques in microalgae, e.g., fluorescence cell-based sensing and "*omics*" approaches (metabolomics, proteomics, genomics), it is now possible to quantify in real time the effects of different stressors on cellular structures of early stages of seaweeds. Thus, it will be possible to track the progressive expression of anti-stress mechanisms along the ontogeny or life cycle phases, an essential approach to understand the adjustments in response to environmental changes at an organismal level.
- *Direct anthropogenic impacts and interaction of multiple stressors*: Warming and ozone depletion are not the only threats to Antarctic biota. Among other concerns are ocean acidification and local decreases in salinity (freshening) due to enhanced melting of glaciers. Furthermore, increase of pollution in the Antarctic environment is generating new and not well-understood threats to these ecosystems. As the identification of sources, concentrations, and persistence of inorganic and organic pollutants poses considerable challenges (reviewed

in Caroli et al. 2001; Bargagli 2005), their effects on seaweeds and their communities are hitherto widely unknown. Moreover, many contaminants are reactive to other environmental factors (e.g., UV radiation), which may enhance their detrimental impact on biota. Because all these different variables are changing simultaneously, the research on the impact of their interactive effects (synergistic, antagonistic, additive, etc.) is challenging (see Chap. 7 by Huovinen and Gómez).

Finally, the contents of this book are in agreement with the increasing awareness of the importance of Antarctic and its biota in global processes and the urgency to improve our understanding on the role and sentinel responses of seaweeds to global climate change. We believe that a comprehensive account of the progress made in the last decades is timely and urgent in order to put into perspective how diversity, ecophysiological adaptations, and ecosystem relations of seaweeds will be molded in the future Antarctica.

References

Amsler CD, Rowley RJ, Laur DR, Quetin LB, Ross RM (1995) Vertical distribution of Antarctic Peninsular macroalgae: cover, biomass, and species composition. Phycologia 34:424–430

Amsler CD, Iken K, McClintock JB, Baker BJ (2011) Defenses of polar microalgae against herbivores and biofoulers. In: Wiencke C (ed) Biology of polar benthic algae. Walter de Gruyter GmbH & Co, KG, Berlin, New York, pp 101–120

Bargagli R (ed) (2005) Antarctic ecosystems: environmental contamination, climate change, and human impact. Springer, Berlin

Barnes DKA, Conlan KE (2012) The dynamic mosaic–disturbance and development of Antarctic benthic communities. In: Rogers AD, Johnston NM, Murphy EJ, Clarke A (eds) Antarctic ecosystems: an extreme environment in a changing world. Wiley, Chichester, UK

Barnes DKA, Fleming A, Sands CJ, Quartino ML, Deregibus D (2018) Icebergs, sea ice, blue carbon and Antarctic climate feedbacks. Philos Trans R Soc A 376 (2122): 20170176

Benning LG, Anesio AM, Lutz S, Tranter M (2014) Biological impact on Greenland's albedo. Nat Geosci 7:691

Bergstrom DM, Convey P, Huiskes AHL (eds) (2006) Trends in Antarctic terrestrial and limnetic ecosystems. Springer, Dordrecht, The Netherlands

Billard E, Reyes J, Mansilla A, Faugeron S, Guillemin M-L (2015) Deep genetic divergence between austral populations of the red alga *Gigartina skottsbergii* reveals a cryptic species endemic to the Antarctic continent. Polar Biol 38:2021–2034

Bronselaer B, Winton M, Griffies SM, Hurlin WJ, Rodgers KB, Sergienko OV, Stouffer RJ, Russell JL (2018) Change in future climate due to Antarctic meltwater. Nature 564:53–58

Brouwer PEM, Geilen EFM, Gremmen NJM, van Lent F (1995) Biomass, cover and zonation patterns of sublittoral macroalgae at Signy Island, South Orkney Islands, Antarctica. Bot Mar 38:259–270

Caroli S, Cescon P, Walton BT (eds) (2001) Environmental contamination in Antarctica, a challenge to analytical chemistry. Elsevier, Amsterdam, London

Clark GF, Stark JS, Palmer AS, Riddle MJ, Johnston EL (2017) The roles of sea-ice, light and sedimentation in structuring shallow Antarctic benthic communities. PLoS One 12(1):e0168391. https://doi.org/10.1371/journal.pone.0168391

Clarke A, Murphy EJ, Meredith MP, King JC, Peck LS, Barnes DKA, Smith RC (2007) Climate change and the marine ecosystem of the western Antarctic Peninsula. Philos Trans R Soc B 362:149–141

Clayton MN (1994) Evolution of the Antarctic benthic algal flora. J Phycol 30:897–904

Constable AJ, Melbourne -Thomas J, Corney SP, Arrigo KR, Barbraud C, Barnes DKA et al (2014) Climate change and Southern Ocean ecosystems. I: how changes in physical habitats directly affect marine biota. Glob Chang Biol 20:3004–3025. https://doi.org/10.1111/gcb.12623

Crame JA (1992) Evolutionary history of the polar regions. Hist Biol 6:37–60

Delépine R, Lamb JM, Zimmermann MH (1966) Preliminary report on the vegetation of the Antarctic Peninsula. Proc Int Seaweed Symp 5:107–116

Deregibus D, Quartino ML, Campana GL, Momo FR, Wiencke C, Zacher K (2016) Photosynthetic light requirements and vertical distribution of macroalgae in newly ice-free areas in Potter Cove, South Shetland Islands, Antarctica. Polar Biol 39:153–166

Drew EA, Hastings RM (1992) A year-round ecophysiological study of *Himantothallus grandifolius* (Desmarestiales, Phaeophyta) at Signy Island, Antarctica. Phycologia 31:262–277

Fraser CI, Morrison AK, Hogg AM, Macaya EC, van Sebille E, Ryan PG, Padovan A, Jack C, Valdivia N, Waters JM (2018) Antarctica's ecological isolation will be broken by storm-driven dispersal and warming. Nat Clim Change 8:704–708. https://doi.org/10.1038/s41558-018-0209-7

Gaudichaud C (1826) Botanique. In: Freycinet L (ed) Voyage autour du monde, entrepons par ordre du Roi, execute sur le corvettes de S.M. l 'Uranie' et la 'Physicienne', pendant les années 1817, 1818, 1819 et 1820. Pillet Aîné, Paris

Gómez I, Thomas DN, Wiencke C (1995) Longitudinal profiles of growth, photosynthesis and light independent carbon fixation in the Antarctic brown alga *Ascoseira mirabilis*. Bot Mar 38:157–164

Gómez I, Weykam G, Klöser H, Wiencke C (1997) Photosynthetic light requirements, daily carbon balance and zonation of sublittoral macroalgae from King George Island (Antarctica). Mar Ecol Prog Ser 148:281–293

Gutkowski R, Maleszewski S (1989) Seasonal changes of the photosynthetic capacity of the Antarctic macroalga *Adenocystis utricularis* (Bory) Skottsberg. Pol Biol 10:145–148

Held C (2014) Chapter 10.5. Phylogeography and population genetics. In: De Broyer C, Koubbi P, Griffiths HJ, Raymond B, d' U d'A C, Van de Putte AP, Danis B, David B, Grant S, Gutt J et al (eds) Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, pp 437–440

Hommersand MH, Moe RL, Amsler CD, Fredericq S (2009) Notes on the systematics and biogeographical relationships of Antarctic and subAntarctic Rhodophyta with descriptions of four new genera and five new species. Bot Mar 52:509–534

Hood E, Battin TJ, Fellman J, O'Neel S, Spencer RGM (2015) Storage and release of organic carbon from glaciers and ice sheets. Nat Geosci 8:91–96

Hooker JD (1847) The botany of the Antarctic voyage of H. M. discovery ships *Erebus* and *Terror* in the years 1839–1843, vol. 1, Flora Antarctica, Part 1 Botany of Lord Auklands Group and Campbell's Island, Part 2 Botany of Fuegia, The Falklands, Kerguelens Land. Reeve Brothers, London

Huovinen P, Gómez I (2013) Photosynthetic characteristics and UV stress tolerance of Antarctic seaweeds along the depth gradient. Polar Biol 36:1319–1332

Huovinen P, Ramírez J, Gómez I (2018) Remote sensing of albedo-reducing snow algae and impurities in the Maritime Antarctica. ISPRS J Photogram Rem Sens 146:507–517

Iken K, Amsler CD, Amsler MO, McClintock JB, Baker BJ (2009) Field studies on deterrent roles of phlorotannins in Antarctic brown algae. Bot Mar 52:547–557

Iñiguez C, Heinrich S, Harms L, Gordillo FJL (2017) Increased temperature and CO_2 alleviate photoinhibition in *Desmarestia anceps*: from transcriptomics to carbon utilization. J Exp Bot 68(14):3971–3984

IPCC (2019) IPCC special report on the ocean and cryosphere in a changing climate. Pörtner H-O, Roberts DC, Masson-Delmotte V, Zhai P, Tignor M, Poloczanska E, Mintenbeck K, Nicolai M, Okem A, Petzold J, Rama B, Weyer N (eds)

Kanao M, Genti Toyokuni G, Yamamoto M-Y (eds) (2018) Antarctica–a key to global change. IntechOpen. https://doi.org/10.5772/intechopen.82197

Klöser H, Ferreyra G, Schloss I, Mercuri G, Laturnus F, Curtosi A (1993) Seasonal variation of algal growth conditions in sheltered Antarctic bays: the example of Potter Cove (King George Island, South Shetlands). J Mar Syst 4:289–301

Klöser H, Quartino ML, Wiencke C (1996) Distribution of macroalgae and macroalgal communities in gradients of physical conditions in Potter Cove, King George Island, Antarctica. Hydrobiologia 333:1–17

Krause-Jensen D, Duarte CM (2016) Substantial role of macroalgae in marine carbon sequestration. Nat Geosci 9(10):737

Lamb IM, Zimmermann MH (1977) Benthic marine algae of the Antarctic Peninsula. Ant Res Ser 23:130–229

Meredith MP, King JC (2005) Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. Geophys Res Lett 32:L19604. https://doi.org/10.1029/2005GL024042

Meredith MP, Falk U, Bers AV, Mackensen A, Schloss IR, Ruiz Barlett E, Jerosch K, Silva Busso A, Abele D (2018) Anatomy of a glacial meltwater discharge event in an Antarctic cove. Phil Trans R Soc A 376:20170163. https://doi.org/10.1098/rsta.2017.0163

Moe R, Henry EC (1982) Reproduction and early development of *Ascoseira mirabilis* Skottsberg (Phaeophyta), with notes on Ascoseirales Petrov. Phycologia 21:55–56

Mormède S, Irisson JO, Raymond B (2014) Chapter 2.3. Distribution modelling. In: De Broyer C, Koubbi P, Griffiths HJ, Raymond B, Udekem d'Acoz C d', Van de Putte AP, Danis B, David B, Grant S, Gutt J et al (eds) Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, pp 27–29

Neushul M (1965) Diving observations of subtidal Antarctic marine vegetation. Bot Mar 8:234–243

Ortiz M, Hermosillo-Nuñez B, González J, Rodríguez-Zaragoza F, Gómez I, Jordán F (2017) Quantifying keystone species complexes: Ecosystem-based conservation management in the King George Island (Antarctic Peninsula). Ecol Ind 81: 453-460

Quartino ML, Deregibus D, Campana GL, Edgar G, Latorre J, Momo FR et al (2013) Evidence of macroalgal colonization on newly ice-free areas following glacial retreat in Potter Cove (South Shetland Islands), Antarctica. PLoS One 8:e58223

Rogers AD, Johnston NM, Murphy EJ, Clarke A (eds) (2012) Antarctic ecosystems: an extreme environment in a changing world. Wiley, Chichester, UK

Schloss IR, Abele D, Moreau S, Demers S, Bers AV, Gonzalez O, Ferreyra GA (2012) Response of phytoplankton dynamics to 19-year (1991–2009) climate trends in Carlini Station (Antarctica). J Mar Syst 92:53–66. https://doi.org/10.1016/j.jmarsys.2011.10.006

Schwarz A, Hawes I, Andrew N, Norkko A, Cummings V, Thrush S (2003) Macroalgal photosynthesis near the southern global limit for growth, Cape Evans, Ross Sea, Antarctica. Polar Biol 26:789–799

Skottsberg K (1907) Zur Kenntnis der subantarktischen und antarktischen Meeresalgen. I. Phaeophyceen. In: Nordenskjöld O (ed) Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition 1901–1903, vol 4: 1. Lithographisches Institut des Generalstabs, Stockholm, pp 1–172

Tedesco M, Doherty S, Fettweis X, Alexander P, Jeyaratnam J, Stroeve J (2016) The darkening of the Greenland ice sheets: trends, drivers, and projections (1981–2100). Cryosphere 10:477–496. https://doi.org/10.5194/tc-10-477-2016

Tedstone AJ, Bamber JL, Cook JM, Williamson CJ, Fettweis X, Hodson AJ, Tranter M (2017) Dark ice dynamics of the south-west Greenland ice sheet. Cryosphere 11:2491–2506. https://doi.org/10.5194/tc-11-2491-2017

Tin T, Liggett D, Maher PT, Lamers M (2014) Antarctic futures: human engagement with the Antarctic environment. Springer, The Netherlands

Turner J, Lu H, White I, King JC, Phillips T, Hosking JS, Bracegirdle TJ, Marshall GJ, Mulvaney R, Deb P (2016) Absence of 21st century warming on Antarctic Peninsula consistent with natural variability. Nature 535:411–415

Valdivia N, Díaz MJ, Garrido I, Gómez I (2015) Consistent richness-biomass relationship across environmental stress gradients in a marine macroalgal-dominated subtidal community on the Western Antarctic Peninsula. Plos One 10(9):e0138582

Van Oppen MJH, Olsen JL, Stam WT, Van der Hoek C, Wiencke C (1993) Arctic–Antarctic disjunction in the benthic seaweeds *Acrosiphonia arcta* (Chlorophyta) and *Desmarestia viridis* (Phaeophyta) are of recent origin. Mar Biol 115:381–386

Vaughan DG, Marshall GJ, Connolley WM, Parkinson CL, Mulvaney R, Hodgson DA, King JC, Pudsey CJ, Turner J (2003) Recent rapid regional climate warming on the Antarctic Peninsula. Clim Change 60:243–274. https://doi.org/10.1023/A:1026021217991

Wadham JL, Hawkings JR, Tarasov L, Gregoire LJ, Spencer RGM, Gutjahr M, Ridgwell A, Kohfeld KE (2019) Ice sheets matter for the global carbon cycle. Nat Comm 10 (1)

Wiencke C (1988) Notes on the development of some benthic marine macroalgae of King George Island, Antarctica. Ser Cient INACh 37:23–47

Wiencke C (1990) Seasonality of brown macroalgae from Antarctica- a long-term culture study under fluctuating Antarctic daylengths. Polar Biol 10:589–600

Wiencke C (1996) Recent advances in the investigation of Antarctic macroalgae. Polar Biol 16:231–240

Wiencke C, Amsler CD, Clayton MN (2014) Chapter 5.1 Macroalgae. In: de Broyer C, Koubbi P, Griffiths HJ, Raymond B, Udekem d'Acoz Cd', Van de Putte PAP, Danis B, David B, Grant S, Gutt J et al (eds) Biogeographic atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, pp 66–73

Zacher K, Wulff A, Molis M, Hanelt D, Wiencke C (2007) UV radiation and consumer effects on a field-grown intertidal macroalgal assemblages in Antarctica. Glob Chang Biol 13:1201–1215

Zaneveld JS (1966) Vertical zonation of Antarctic and subAntarctic benthic marine algae. Antarctic J US 1(5):211–213

Zielinski K (1981) Benthic macroalgae of Admiralty Bay (King George Island, South Shetland Islands) and circulation of algal matter between the water and the shore. Pol Polar Res 2:71–94

Zielinski K (1990) Bottom macroalgae of the Admiralty Bay (King George Island, South Shetlands, Antarctica). Pol Polar Res 11:95–131