Chapter 13
Seaweeds and Their Communities in Polar Regions

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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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References

Adey WH, Lindstrom SC, Hommersand MH, Müller KM (2008) The biogeographic origin of Arctic endemic seaweeds: a thermogeographic view. J Phycol 44:1384–1394

Aguilera J, Bischof K, Karsten U, Hanelt D, Wiencke C (2002) Seasonal variation in ecological patterns in macroalgae from an Arctic fjord II. Pigment accumulation and biochemical defence systems against high light stress. Mar Biol 140:1087–1095

Alongi G, Cormaci M, Furnari G (2002) The Corallinaceae (Rhodophyta) from the Ross Sea (Antarctica): a taxonomic revision rejects all records except *Phymatolithon foecundum*. Phycologia 41:140–146

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, McClintock JB, Baker BJ (1998) Chemical defense against herbivory in the Antarctic marine macroalgae *Iridaea cordata* and *Phyllophora antarctica* (Rhodophyceae). J Phycol 34:53–59

Amsler CD, McClintock JB, Baker BJ (1999) An antarctic feeding triangle: defensive interactions between macroalgae, sea urchins, and sea anemones. Mar Ecol Prog Ser 183:105–114

Amsler CD, Iken K, McClintock JB, Amsler MO, Peters KJ, Hubbard JM, Furrow FB, Baker BJ (2005a) Comprehensive evaluation of the palatability and chemical defenses of subtidal macroalgae from the Antarctic Peninsula. Mar Ecol Prog Ser 294:141–159

Amsler CD, Okogbue IN, Landry DM, Amsler MO, McClintock JB, Baker BJ (2005b) Potential chemical defenses against diatom fouling in Antarctic macroalgae. Bot Mar 48:318–322

Amsler CD, McClintock JB, Baker BJ (2008) Macroalgal chemical defenses in polar marine communities. In: Amsler CD (ed) Algal chemical ecology. Springer, Berlin, pp 91–103

Amsler CD, Amsler MO, McClintock JB, Baker BJ (2009) Filamentous algal endophytes in macrophytic Antarctic algae: prevalence in hosts and palatability to mesoherbivores. Phycologia 48:324–334

Amsler CD, Iken K, McClintock JB, Baker BJ (2011) Defenses of polar macroalgae against herbivores and biofoulers. In: Wiencke C (ed) Biology of polar benthic algae. De Gruyter, Berlin, pp 101–120

Andersson B, Salter AH, Virgin I, Vass I, Styring S (1992) Photodamage to photosystem II-primary and secondary events. J Photochem Photobiol B: Biol 15:15–31

Apt KE (1988) Ethiology and development of hyperplasia induced by *Streblonema* sp. (Phaeophyta) on members of the Laminariales (Phaeophyta). J Phycol 24:28–34

Aro EM, Virgin I, Andersson B (1993) Photoinhibition of photosystem II. Inactivation, protein damage and turnover. Biochim Biophys Acta 1143:113–134

Aumack CF, Amsler CD, McClintock JB, Baker BJ (2010) Chemically mediated resistance to mesoherbivory in finely branched macroalgae along the western Antarctic Peninsula. Eur J Phycol 45:19–26

Aumack CF, Amsler CD, McClintock JB, Baker BJ (2011) Impacts of mesograzers on epiphyte and endophyte growth associated with chemically defended macroalge from the western Antarctic Peninsula: a mesocosm experiment. J Phycol 47:36–41

Barnes D, Brockington S (2003) Zoobenthic biodiversity, biomass and abundance at Adelaide Island. Antarctica Mar Ecol Prog Ser 249:145–155

Becker EW (1982) Physiological studies on Antarctic *Prasiola crispa* and *Nostoc commune* at low temperatures. Polar Biol 1:99–104

Becker S, Walter B, Bischof K (2011) Freezing tolerance and photosynthetic performance of polar seaweeds at low temperatures. In: Wiencke C (ed) Biology of Polar Benthic Algae. De Gruyter, Berlin, pp 221–236

Beuchel F, Gulliksen B (2008) Temporal patterns of benthic community development in an Arctic fjord (Kongsfjorden, Svalbard): results of a 24-year manipulation study. Polar Biol 31:913–924

Bischoff B, Wiencke C (1993) Temperature requirements for growth and survival of macroalgae from Disko-Island (Greenland). Helgol Mar Res 47:167–191

Bischoff B, Wiencke C (1995) Temperature ecotypes and biogeography of Acrosiphoniales (Chlorophyta) with Arctic-Antarctic disjunct and Arctic/cold-temperate distributions. Eur J Phycol 30:19–27

Bischoff-Bäsmann B, Wiencke C (1996) Temperature requirements for growth and survival of Antarctic Rhodophyta. J Phycol 32:525–535

Bolton JJ, Lüning K (1983) Optimal growth and maximal survival temperatures of Atlantic *Laminaria* species (Phaeophyta) in culture. Mar Biol 66:89–94

Bowden DA (2005) Quantitative characterization of shallow marine benthic assemblages at Ryder Bay, Adelaide Island. Antarctica. Mar Biol 146:1235–1249

Brouwer PEM (1996a) In situ photosynthesis and estimated annual production of the red macroalga *Myriogramme mangini* in relation to underwater irradiance at Signy Island (Antarctica). Antarctic Sci 8:245–252

Brouwer PEM (1996b) Decomposition in situ of the sublittoral Antarctic macroalga *Desmarestia anceps* Montagne. Polar Biol 16:129–137

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

Busdosh M, Beehler CL, Robillard GA, Tarbox KR (1983) Distribution and abundance of kelp in the Alaskan Beaufort Sea near Prudhoe Bay. Arctic 38:18–22

Campana GL, Zacher K, Fricke F, Molis M, Wulff A, Quartino ML, Wiencke C (2011) Drivers of colonization and succession in polar benthic macro- and microalgal communities. In: Wiencke C (ed) Biology of polar benthic algae. De Gruyter, Berlin, pp 299–320

Cattaneo-Vietti R, Chiantore M, Gambi MC, Albertelli G, Cormaci M, Di Geronimo I (2000) Spatial and vertical distribution of benthic littoral communities in Terra Nova Bay. In: Faranda FM, Guglielmo L, Ianora A (eds) Ross sea ecology. Italiantartide expeditions (1985–1995). Springer, Berlin, pp 503–514

Chapman ARO, Lindley JE (1980) Seasonal growth of *Laminaria solidungula* in the Canadian high Arctic in relation to irradiance and dissolved nutrient concentration. Mar Biol 57:1–5

Chung H, Oh YS, Lee IK, Kim D-Y (1994) Macroalgal vegetation of Maxwell Bay in King George Island. Antarctica Korean J Phycol 9:47–58

Clarke DL (1990) Arctic Ocean ice cover; Geologic history and climatic significance. In: Grantz A, Johnson L, Sweeney JL (eds) The arctic ocean region. Geol Soc, America, Boulder Colorado, pp 53–62

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-Biol Sci 362:149–166

Corbisier TN, Petti MAV, Skowronski RSP, Brito TAS (2004) Trophic relationships in the nearshore zone of Martel Inlet (King George Island, Antarctica): $\delta^{13}C$ stable-isotope analysis. Polar Biol 27:75–82

Cormaci M, Furnari G, Scammacca B (2000) The macrophytobenthos of Terra Nova Bay. In: Faranda FM, Guglielmo L, Ianora A (eds) Ross Sea Ecology. Italiantartide Expeditions (1987-1995). Springer, Berlin, pp 493-502

Correa JA, Sánchez PA (1996) Ecological aspects of algal infectious diseases. Hydrobiologia 326–327:89–95

Crame JA (1993) Latitudinal range fluctuations in the marine realm through geological time. Trends Ecol Evol 8:162–266

Dawson R, Schramm W, Bolter M (1985) Factors influencing the production, decomposition and distribution of organic matter in Admirality Bay, King George Island. In: Siegfried WR, Condy PR, Laws RM (eds) Antarctic nutrient cycles and food webs. Springer, Berlin, pp 109–114

DeLaca TE, Lipps JH (1976) Shallow water marine associations. Antarctic Peninsula. Antarctic J US 11:12–20

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

Dhargalkar V, Reddy C, Deshmukhe G, Unatawale A (1987) Biochemical composition of some benthic marine algae of the Vestfold Hills, Antarctica. Indian J Mar Sci 16:269–271

Dhargalkar V, Burton H, Kirkwood J (1988) Animal associations with the dominant species of shallow water macrophytes along the coastline of the Vestfold Hills, Antarctica. Hydrobiologia 165:141–150

Dieckmann G, Reichardt W, Zielinski D (1985) Growth and production of the seaweed, *Himantothallus grandifolius*, at King George Island. In: Siegfried WR, Condy P, Laws RM (eds) Antarctic nutrient cycles and food webs. Springer, Berlin, pp 104–108

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

Dring MJ (2006) Stress resistance and disease resistance in seaweeds: The role of reactive oxygen metabolism. Adv Bot Res 43:175–207

Ducklow HW, Baker K, Martinson DG, Quetin LB, Ross RM, Smith RC, Stammerjohn SE, Vernet M, Fraser W (2007) Marine pelagic ecosystems: the west Antarctic Peninsula. Philos Trans R Soc B 362:67–94

Dummermuth AL, Wiencke C (2003) Experimental investigation of seasonal development in six Antarctic red macroalgae. Antarct Sci 15:449–457

Dunton KH (1985) Growth of dark-exposed *Laminaria saccharina* (L.) Lamour and *Laminaria solidungula* J. Ag (Laminariales: Phaeophyta) in the Alaskan Beaufort Sea. J Exp Mar Biol Ecol 94:181–189

Dunton KH (1990) Growth and production in *Laminaria solidungula*: relation to continuous underwater light levels in the Alaskan high Arctic. Mar Biol 106:297–304

Dunton KH (1992) Arctic biogeography: The paradox of the marine benthic fauna and flora. Trends Ecol Evol 7:183–189

Dunton K (2001) d^{15}N and d^{13}C measurements of Antarctic Peninsula fauna: trophic relationships and assimilation of benthic seaweeds. Am Zool 41:99–112

Dunton KH, Schell DM (1986) Seasonal carbon budget and growth of *Laminaria solidungula* in the Alaskan High Arctic Mar. Ecol Prog Ser 31:57–66

Dunton KH, Schell DM (1987) Dependence of consumers on macroalgal (*Laminaria solidungula*) carbon in an arctic kelp community. d^{13}C evidence. Mar Biol 93:615–625

Dunton KH, Schonberg SV (2000) The benthic faunal assemblage of the Boulder Patch kelp community. In: Johnson SR, Truett JC (eds) The natural history of an arctic oil field. Academic, San Diego, pp 372–397

Dunton KH, Reimnitz E, Schonberg S (1982) An Arctic kelp community in the Alaskan Beaufort Sea. Arctic 35:465–484

Elner R, Vadas RJ (1990) Inference in ecology: the sea urchin phenomenon in the northwest Atlantic. Am Nat 136:108–125

Estes J, Duggins D (1995) Sea otter and kelp forests in Alaska: generality and variation in a community ecological paradigm. Ecol Monogr 65:75–100

Feely RA, Sabine CL, Lee K, Berelson W, Kleypas J, Fabry VJ, Millero FJ (2004) Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. Science 305:362–366

Fischer G, Wiencke C (1992) Stable carbon isotope composition, depth distribution and fate of macroalgae from the Antarctic Peninsula region. Polar Biol 12:341–348

Giordano MJ, Beardall J, Raven JA (2005) CO_2 concentrating mechanisms in algae: mechanisms, environmental modulation, and evolution. Annu Rev Plant Biol 56:99–131

Gómez I, Wiencke C (1997) Seasonal growth and photosynthetic performance of the Antarctic macroalga *Desmarestia menziesii* (Phaeophyceae) cultivated under fluctuating Antarctic daylengths. Bot Acta 110:25–31

Gómez I, Wiencke C, Weykam G (1995) Seasonal photosynthetic characteristics of the brown alga *Ascoseira mirabilis* from King George Island (Antarctica). Mar Biol 123:167–172

Gómez I, Wiencke C, Thomas DN (1996) Variations in photosynthetic characteristics of the Antarctic marine brown alga *Ascoseira mirabilis* in relation to thallus age and size. Eur J Phycol 31:167–172

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 Progr Ser 148:281–293

Gómez I, Wulff A, Roleda MY, Huovinen P, Karsten U, Quartino ML, Dunton K, Wiencke C (2011) Light and temperature demands of marine benthic microalgae and seaweeds in polar regions. In: Wiencke C (ed) Biology of polar benthic algae. De Gruyter, Berlin, pp 195–220

Hanelt D (1998) Capability of dynamic photoinhibition in Arctic macroalgae is related to their depth distribution. Mar Biol 131:361–369

Hanelt D, Jaramillo J, Nultsch W, Senger S, Westermeier R (1994) Photoinhibitioin as a regulative mechanism of photosynthesis in marine algae of Antarctica. Ser Cient INACH 44:67–77

Hanelt D, Melchersmann B, Wiencke C, Nultsch W (1997) Effects of high light stress on photosynthesis of polar macroalgae in relation to depth distribution. Mar Ecol Prog Ser 149:255–266

Hanelt D, Tüg H, Bischof K, Gross C, Lippert H, Sawall T, Karsten U, Wiencke C (2001) Light regime in an Arctic fjord: a study related to stratospheric ozone depletion as a basis for determination of UV effects on algal growth. Mar Biol 138:649–658

Henley WJ, Dunton KH (1995) A seasonal comparison of carbon, nitrogen, and pigment content in *Laminaria solidungula* and *L. saccharina* (Phaeophyta) in the Alaskan Arctic. J Phycol 31:325–331

Hommersand MH, Moe RL, Amsler CD, Fredericq S (2011) Notes on the systematics and biogeographical relationships of Antarctic and sub-Antarctic Rhodophyta with descriptions of four new genera and five new species. In: Wiencke C (ed) Biology of Polar Benthic Algae. De Gruyter, Berlin, pp 53–100

Hop H, Pearson T, Hegseth EN, Kovacs KM, Wiencke C, Kwasniewski S, Eiane K, Mehlum F, Gulliksen B, Wlodarska-Kowalczuk M, Lydersen C, Weslawski JM, Cochrane S, Gabrielsen GW, Leakey RJG, Lønne OJ, Zajaczkowski M, Falk-Petersen S, Kendall M, Wängberg S-Å, Bischof K, Voronkov AY, Kovaltchouk NA, Wiktor J, Poltermann M, di Prisco G, Papucci C, Gerland S (2002) The marine ecosystem of Kongsfjorden. Svalbard Polar Res 21:167–208

Horn M, Neighbors M (1984) Protein and nitrogen assimilation as a factor in predicting the seasonal macroalgal diet of the monkeyface prickleback. Trans Amer Fish Soc 113:388–396

Huang YM, Amsler MO, McClintock JB, Amsler CD, Baker BJ (2007) Patterns of gammarid amphipod abundance and species composition associated with dominant subtidal macroalgae along the western Antarctic Peninsula. Polar Biol 30:1417–1430

Iken K (1999) Feeding ecology of the Antarctic herbivorous gastropod *Laevilacunaria antarctica* Martens. J Exp Mar Biol Ecol 236:133–148

Iken K, Amsler CD, Amsler MO, McClintock JB, Baker BJ (2011) Field studies on deterrent properties of phlorotannins in Antarctic brown algae. In: Wiencke C (ed) Biology of Polar Benthic Algae. De Gruyter, Berlin, pp 121–140

Irving A, Connell S, Johnston E, Pile A, Gillanders B (2005) The response of encrusting coralline algae to canopy loss: an independent test of predictions on an Antarctic coast. Mar Biol 147:1075–1083

Jacob A, Kirst GO, Wiencke C, Lehmann H (1991) Physiological responses of the Antarctic green alga *Prasiola crispa* ssp. *antarctica* to salinity stress. J. Plant Physiol 139:57–62

Jacob A, Wiencke C, Lehmann H, Kirst GO (1992) Physiology and ultrastructure of desiccation in the green alga *Prasiola crispa* from Antarctica. Bot Mar 35:297–303

Johnston E, Connell S, Irving A, Pile A, Gillanders B (2007) Antarctic patterns of shallow subtidal habitat and inhabitants in Wilke's Land. Polar Biol 30:781–788

Kain JM (1989) The seasons in the subtidal. Br Phycol J 24:203–215

Karsten U, Wiencke C, Kirst GO (1991a) The effect of salinity changes upon physiology of eulittoral green macroalgae from Antarctica and Southern Chile. I. Cell viability, growth, photosynthesis and dark respiration. J. Plant Physiol 138:667–673

Karsten U, Wiencke C, Kirst GO (1991b) The effect of salinity changes upon physiology of eulittoral green macroalgae from Antarctica and Southern Chile II. Inorganic ions and organic compounds. J Exp Bot 42:1533–1539

Karsten U, Kück K, Vogt C, Kirst GO (1996) Dimethylsulfoniopropionate production in phototrophic organisms and its physiological function as a cryoprotectant. In: Kiene RP (ed) Biological and environmental chemistry of DMSP and related sulfonium compounds. Plenum, New York, pp 143–153

Karsten U, Bischof K, Wiencke C (2001) Photosynthetic performance of Arctic macroalgae after transplantation from deep to shallow waters. Oecologia 127:11–20

Karsten U, Wulff A, Roleda MY, Müller R, Steinhoff FS, Fredersdorf J, Wiencke C (2011) Physiological responses of polar benthic algae to ultraviolet radiation. In: Wiencke C (ed) Biology of polar benthic algae. De Gruyter, Berlin, pp 271–298

Kirkwood J, Burton H (1988) Macrobenthic assemblages in Ellis Fjord, Vestfold Hills. Antarctica Mar Biol 97:445–457

Kirst GO (1990) Salinity tolerance of eukaryotic marine algae. Annu Rev Plant Physiol Plant Mol Biol 41:21–53

Klöser H, Mercuri G, Laturnus F, Quartino ML, Wiencke C (1994) On the competive balance of macroalgae at Potter Cove (King George Island, South Shetlands). Polar Biol 14:11–16

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

Lamb IM, Zimmerman MH (1977) Benthic marine algae of the Antarctic Peninsula. Antarctic Research Series 5:130–229

Lawver LA, Sclater JG, Meinke M (1985) Mesozoic and Cenozoic Reconstructions of the South Atlantic. Tectonophysics 114:233–254

Leclerc N, Gattuso JP, Jaubert J (2000) CO_2 partial pressure controls the calcification rate of a coral community. Global Change Biol 6:329–334

Liebezeit G, von Bodungen B (1987) Biogenic fluxes in the Bransfield Strait: Planktonic *versus* macroalgal sources. Mar Ecol Prog Ser 36:23–32

Lippert H, Iken K, Rachor E, Wiencke C (2001) Macrofauna associated with macroalgae in the Kongsfjord (Spitsbergen). Polar Biol 24:512–522

Lowell RB, Markham JH, Mann KH (1991) Herbivore-like damage induces increased strength and toughness in a seaweed. Proc R Soc London: Biol Sci 243:31–38

Lüder UH, Knoetzel J, Wiencke C (2001a) Acclimation of photosynthesis and pigments to seasonally changing light conditions in the endemic Antarctic red macroalga *Palmaria decipiens*. Polar Biol 24:598–603

Lüder UH, Knoetzel J, Wiencke C (2001b) Two forms of phycobilisomes in the Antarctic red macroalga *Palmaria decipiens* (Palmariales, Florideophyceae). Physiol Plant 112:572–581

Lüder UH, Knoetzel J, Wiencke C (2002) Acclimation of photosynthesis and pigments during and after six months of darkness in *Palmaria decipiens* (Rhodophyta)—a study to simulate Antarctic winter sea ice cover. J Phycol 38:904–913

Lüning K (1988) Photoperiodic control of sorus formation in the brown alga *Laminaria saccharina*. Mar Ecol Prog Ser 45:137–144

Lüning K (1990) Seaweeds—their environment, biogeography and ecophysiology. Wiley, New York

Lüning K (1991) Circannual growth rhythm in a brown alga. *Pterygophora californica*. Bot Acta 104:157–162

Lüning K, Dring MJ (1979) Continuous underwater light measurement near Helgoland (North Sea) and its significance for characteristic light limits in the sublittoral region. Helgol Meeresunters 32:403–424

Lüning K, Kadel P (1993) Daylength range for circannual rhythmicity in *Pterygophora californica* (Alariaceae, Phaeophyta) and synchronisation of seasonal growth by daylength cycles in several other brown algae. Phycologia 32:379–387

McClintock JB, Ducklow H, Fraser W (2008) Ecological responses to climate change on the Antarctic Peninsula. Am Sci 96:302–310

McClintock JB, Angus RA, McDonald MR, Amsler CD, Catledge SA, Vohra YK (2009) Rapid dissolution of shells of weakly calcified Antarctic benthic macroorganisms indicates high vulnerability to ocean acidification. Antarct Sci 21:449–456

Miller KA, Pearse JS (1991) Ecological studies of seaweeds in McMurdo Sound. Antarctica. Am Zool 31:35–48

Moe RL, DeLaca TE (1976) Occurrence of macroscopic algae along the Antarctic Peninsula. Antarctic J US 11:20–24

Molis M, Wessels H, Hagen W, Karsten U, Wiencke C (2008) Do sulphuric acid and the brown alga *Desmarestia viridis* support community structure in Arctic kelp patches by altering grazing impact, distribution patterns, and behaviour of sea urchins? Polar Biol 32:71–82

Müller R, Laepple T, Bartsch I, Wiencke C (2011) Impact of oceanic warming on the distribution of seaweeds in polar and cold-temperate waters. In: Wiencke C (ed) Biology of polar benthic algae. de Gruyter, New York, pp 237–270

Neushul M (1965) Diving observation of sub-tidal Antarctic marine vegetation. Bot Mar 8:234–243

Norkko A, Thrush SF, Cummings VJ, Funnell GA, Schwarz AM, Andrew NL, Hawes I (2004) Ecological role of *Phyllophora antarctica* drift accumulations in coastal soft-sediment communities of McMurdo Sound. Antarctica Polar Biol 27:482–494

Novaczek I, Lubbers GW, Breeman AM (1990) Thermal ecotypes in amphi-Atlantic algae. I. Algae of Arctic to cold-temperate distribution (*Chaetomorpha melagonium*, *Devaleraea ramentacea* and *Phycodrys rubens*). Helgoländer Meeresunters 44:459–474

Pedersen PM (1976) Marine, benthic algae from southernmost Greenland. Meddr Grønland 3:1–80, 7 plates

Peters AF (2003) Molecular identification, taxonomy and distribution of brown algal endophytes, with emphasis on species from Antarctica. Proc Int Seaweed Symp 17:293–302

Peters AF, Breeman AM (1993) Temperature tolerance and latitudinal range of brown algae from temperate Pacific South America. Mar Biol 115:143–150

Peters AF, Schaffelke B (1996) *Streblonema* (Ectocarpales, Phaeophyceae) infection in the kelp *Laminaria saccharina* (Laminariales, Phaeophyceae) in the western Baltic. Hydrobiologia 326–327:111–116

Peters AF, van Oppen MJH, Wiencke C, Stam WT, Olsen JL (1997) Phylogeny and historical ecology of the Desmarestiaceae (Phaeophyceae) support a Southern Hemisphere origin. J Phycol 33:294–309

Peters KJ, Amsler CD, Amsler MO, McClintock JB, Dunbar RB, Baker BJ (2005) A comparative analysis of the nutritional and elemental composition of macroalgae from the western Antarctic Peninsula. Phycologia 44:453–463

Quartino ML, Boraso de Zaixso AL (2008) Summer macroalgal biomass in Potter Cove, South Shetland Islands. Antarctica: its production and flux to the ecosystem. Polar Biol 31:281–294

Quartino ML, Klöser H, Schloss IR, Wiencke C (2001) Biomass and associations of benthic marine macroalgae from the inner Potter Cove (King George Island, Antarctica) related to depth and substrate. Polar Biol 24:349–355

Rakusa-Suszczewski S, Zielinski K (1993) Macrophytobenthos. In: Rakusa-Suszczewski S (ed) The maritime Antarctic coastal ecosystem of Admiralty Bay. Polish Academy of Sciences, Warsaw, pp 57–60

Raymond JA, Fritsen CH (2001) Semipurification and ice recrystallization inhibition activity of ice-active substances associated with Antarctic photosynthetic organisms. Cryobiology 43:63–70

Raymond JA, Knight CA (2003) Ice binding, recrystallization inhibition, and cryoprotective properties of ice-active substances associated with Antarctic sea ice diatoms. Cryobiology 46:174–181

Reichardt W (1987) Burial of antarctic macroalgal debris in bioturbated deep-sea sediments. Deep-Sea Res 34:1761–1770

Richardson MG (1977) The ecology including physiological aspects of selected Antarctic marine invertebrates associated with inshore macrophytes. PhD Dissertation. Department of Zoology, University of Durham

Richter A, Wuttke S, Zacher K (2008) Two years of in situ UV measurements at the Dallmann Laboratory/Jubany Station. Ber Polarforsch Meeresforsch 571:12–19

Roleda MY (2009) Photosynthetic response of Arctic kelp zoospores exposed to radiation and thermal stress. Photochem Photobiol Sci 8:1302–1312

Roleda MY, Wiencke C, Hanelt D, Bischof K (2007) Sensitivity of the early life stages of macroalgae from the northern hemisphere to ultraviolet radiation. Photochem Photobiol 83:1–12

Schaffelke B, Lüning K (1994) A circannual rhythm controls seasonal growth in the kelp *Laminaria hyperborea* and *L. digitata* from Helgoland (North Sea). Eur J Phycol 29:49–56

Schwarz AM, 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

Sevak HP (2010) Potential chemical defenses against diatom fouling in macroalgae from the Antarctic Peninsula: insights from bioassay guided fractionation. MS Thesis. Department of Biology, University of Alabama at Birmingham

Smith RC, Stammerjohn SE (2001) Variations of surface air temperature and sea-ice extent in the western Antarctic Peninsula region. Ann Glaciol 33:493–500

Stammerjohn S E, Martinson DG, Smith RC, Yuan X, Rind D (2008) Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño–Southern Oscillation and Southern Annular Mode variability, J Geophys Res 113:C03S90, doi:10.1029/2007JC004269.

Svendsen H, Beszczynska-Møller A, Hagen JO, Lefauconnier B, Tverberg V, Gerland S, Bischof K, Papucci C, Ørbæk JB, Zajaczkowski M, Azzolini R, Bruland O, Wiencke C, Winther JG, Dallmann W (2002) The physical environment of Kongsfjorden-Krossfjorden, an Arctic fjord system in Svalbard. Polar Res 21:133–166

tom Dieck I (1992) North Pacific and North Atlantic digitate *Laminaria* species (Phaeophyta): hybridisation experiments and temperature responses. Phycologia 31:147–163

tom Dieck I (1993) Temperature tolerance and survival in darkness of kelp gametophytes (Laminariales, Phaeophyta): ecological and biogeographical implications. Mar Ecol Prog Ser 100:253–264

van den Hoek C (1982a) Phytogeographic distribution groups of benthic marine algae in the North Atlantic Ocean. A review of experimental evidence from life history studies. Helgoländer Meeresunters 35:153–214

van den Hoek C (1982b) The distribution of benthic marine algae in relation to the temperature regulation of their life histories. Biol J Linn Soc 18:1–144

van Oppen MJH, Olsen JL, Stam W, van den Hoek C, Wiencke C (1993) Arctic-Antarctic disjunctions in the benthic seaweeds *Acrosiphonia arcta* (Chlorophyta) and *Desmarestia viridis/willii* (Phaeophyta) are of recent origin. Mar Biol 115:381–386

van Oppen MJH, Diekmann OE, Wiencke C, Stam WT, Olsen JL (1994) Tracking dispersal routes: Phylogeography of Arctic-Antarctic disjunct seaweed *Acrosiphonia arcta* (Chlorophyta). J Phycol 30:67–80

Wessels H, Hagen W, Molis M, Wiencke C, Karsten U (2006) Intra- and interspecific differences in palatability of Arctic macroalgae from Kongsfjorden (Spitsbergen) for two benthic sympatric invertebrates. J Exp Mar Biol Ecol 329:20–33

Weykam G, Gómez I, Wiencke C, Iken K, Kloser H (1996) Photosynthetic characteristics and C:N ratios of macroalgae from King George Island (Antarctica). J Exp Mar Biol Ecol 204:1–22

Weykam G, Thomas DN, Wiencke C (1997) Growth and photosynthesis of the Antarctic red algae *Palmaria decipiens* (Palmariales) and *Iridaea cordata* (Gigartinales) during and following extended periods of darkness. Phycologia 36:395–405

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

Wiencke C (1990b) Seasonality of red and green macroalgae from Antarctica - a long-term culture study under fluctuating Antarctic daylengths. Polar Biol 10:601–607

Wiencke C, Clayton MN (2002) Antarctic Seaweeds. ARG Gantner Verlag, KG Ruggell

Wiencke C, Fischer G (1990) Growth and stable carbon isotope composition of cold-water macroalgae in relation to light and temperature. Mar Ecol Prog Ser 65:283–292

Wiencke C, Bartsch I, Bischoff B, Peters AF, Breeman AM (1994) Temperature requirements and biogeography of Antarctic, Arctic and amphiequatorial seaweeds. Bot Mar 37:247–259

Wiencke C, Clayton MN, Langreder C (1996) Life history and seasonal morphogenesis of the endemic Antarctic brown alga *Desmarestia anceps* Montagne. Bot Mar 39:435–444

Wiencke C, Vögele B, Kovaltchouk NA, Hop H (2004) Species composition and zonation of marine benthic macroalgae at Hansneset in Kongsfjorden, Svalbard. Ber Polarforsch Meeresforsch 492:55–62

Wiencke C, Roleda MY, Gruber A, Clayton MN, Bischof K (2006) Susceptibility of zoospores to UV radiation determines upper depth distribution limit of Arctic kelps: evidence through field experiments. J Ecol 94:455–463

Wiencke C, Clayton MN, Gómez I, Iken K, Lüder U, Amsler CD, Karsten U, Hanelt D, Bischof K, Dunton K (2007) Life strategy, ecophysiology and ecology of seaweeds in polar water. Rev Environ Sci Biotech 6:95–126

Wiencke C, Gómez I, Dunton K (2011) Phenology and seasonal physiological performance of polar seaweeds. In: Wiencke C (ed) Biology of Polar Benthic Algae. De Gruyter, Berlin, pp 181–194

Wilce RT (1990) Role of the Arctic Ocean as a bridge between the Atlantic and Pacific Oceans: fact and hypothesis. In: Garbary DJ, South GR (eds) Evolutionary biogeography of the marine algae of the North Atlantic. Springer, Berlin, pp 323–348

Wilce RT (1994) The Arctic subtidal as habitat for macrophytes. In: Lobban CS, Harrison PJ (eds) Seaweed ecology and physiology. Cambridge University Press, Cambridge, pp 89–92

Wilce RT, Pedersen PM, Sekida S (2009) *Chukchia pedicellata* gen. et sp. nov. and *C. endophytica* nov. comb., Arctic endemic brown algae (Phaeophyceae). J Phycol 45:272–286

Włodarska-Kowalczuk M, Kukliński P, Ronowicz M, Legeżyńska J, Gromisz S (2009) Assessing species richness of macrofauna associated with macroalgae in Arctic kelp forests (Hornsund, Svalbard). Polar Biol 32:897–905

Wulff A, Iken K, Quartino ML, Al-Handal A, Wiencke C, Clayton MN (2011) Biodiversity, biogeography and zonation of marine benthic micro- and macroalgae in the Arctic and Antarctic. In: Wiencke C (ed) Biology of polar benthic algae. De Gruyter, Berlin, pp 23–52

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

Zacher K, Rautenberger R, Hanelt D, Wulff A, Wiencke C (2011) The abiotic environment of polar benthic algae. In: Wiencke C (ed) Biology of polar benthic algae. De Gruyter, Berlin, pp 9–22

Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292:686–693

Zamzow JP, Amsler CD, McClintock JB, Baker BJ (2010) Habitat choice and predator avoidance by Antarctic amphipods: the roles of algal chemistry and morphology. Mar Ecol Prog Ser 400:155–163

Zamzow JP, Aumack CF, Amsler CD, McClintock JB, Amsler MO, Baker BJ (2011) Gut contents and stable isotope analyses of the Antarctic fish, *Notothenia coriiceps* Richardson, from two macroalgal communities. Antarctic Sci 23:107–116

Zaneveld JS (1966) The occurrence of benthic marine algae under shore fast-ice in the western Ross Sea, Antarctic. Proc Int Seaweed Symp 5:217–231

Zielinski K (1981) Benthic macroalgae of Admirality Bay (King George Island, South Shetland Islands) and circulation of algal matter between 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