Chapter 10
Life History Strategies, Photosynthesis, and Stress Tolerance in Propagules of Antarctic Seaweeds

Nelso Navarro, Pirjo Huovinen, and Iván Gómez

Abstract Reproduction is one of the most important processes to maintain seaweed populations. In general, growth and reproduction of seaweeds depend on environmental cues, such as change in temperature, light, and nutrients. However, the fact that Antarctic waters show a small variation in temperature and nutrient levels over the year, these biological processes depend mainly on variables related to light conditions, especially daylength. This seems to be more obvious in the eulittoral and shallow sublittoral species, because the reproduction and growth coincides with the spring season. However, in species inhabiting the deeper sublittoral zone, reproduction seems to be controlled by a free-running endogenous clock synchronized by the seasonal variation of daylength or by photoperiodisms. Whatever the case, the Antarctic environment imposes physiological constraints to reproductive output, settlement and development of propagules, recruitment, and growth of seaweeds. Early life stages (e.g., spores, gametes, propagules, and plantlets) are extremely shade-adapted and susceptible to environmental stress, such as exposure to UV radiation; however, they are thermally well adapted, at least for short periods of time, allowing them to develop in a highly variable environment. In this chapter, we review the main reproduction strategies that Antarctic seaweeds display to cope with the extreme environment. Additionally, we review recent studies on stress tolerance of early developmental stages from selected species. In scenarios of the changing Antarctic environment due to warming, UV radiation, freshening, and

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other emergent stressors, the knowledge on adaptive life strategies of early developmental phases can allow us better predicting the fate of seaweed communities.

Keywords Life history stages · Photosynthetic light requirements · Reproduction · Seaweed propagules · Seasonal development

10.1 Seasonal Strategies and Life History Cycles

In their environment, seaweeds are exposed to a complex suite of abiotic variables, whose interaction may affect reproduction synergistically or antagonistically. In the case of Antarctic seaweeds, the life strategy of the individual species is regulated by the strong seasonal variation in light conditions (Wiencke et al. 2009). Two different growth (and reproduction) strategies have been identified: the season anticipator and season responder strategy (sensu Kain 1989; Wiencke and Clayton 2002). These strategies have been corroborated through long-term laboratory culture experiments in which temperature and nutrient levels were kept constant and only light and daylength were modified in order to simulate the seasonally fluctuating Antarctic irradiances (Wiencke 1990a, b; Dummermuth and Wiencke 2003). Moreover, other phenological events such as seasonal induction of propagules, their release, and the growth of early developmental stages have been examined in the field (Roleda et al. 2007, 2008; Zacher et al. 2009; Navarro et al. 2016).

10.1.1 Season Anticipators

This group of algae grows and reproduces in winter under short-day and low-light conditions (Fig. 10.1). Thus, physiological and reproduction processes seem to be controlled by a free-running endogenous annual rhythm synchronized by the seasonal changes of daylength or by photoperiodisms and not by environmental conditions (such as levels of light or temperature) as demonstrated by Lüning and tom Dieck (1989), tom Dieck (1989), and Lüning and Kadel (1993) in several species from temperate regions. Likewise, the growth of Antarctic season anticipators has been related to increasing daylength during the late winter and early spring (Wiencke et al. 2007, 2009). Many endemic Antarctic seaweeds with sublittoral distribution are regarded as season anticipators, e.g., the brown seaweeds *Himantothallus grandifolius* (A.Gepp and E.S.Gepp) Zinova, *Desmarestia anceps* Montagne, *D. antarctica* Moe *et* Silva, *Phaeurus antarcticus* Skottsberg (Wiencke 1990a), *Ascoseira mirabilis* Skottsberg (Gómez et al. 1995, 1996; Wiencke 1990a), and *D. menziesii* J. Agardh (Gómez and Wiencke 1996) and the red seaweeds *Palmaria decipiens*

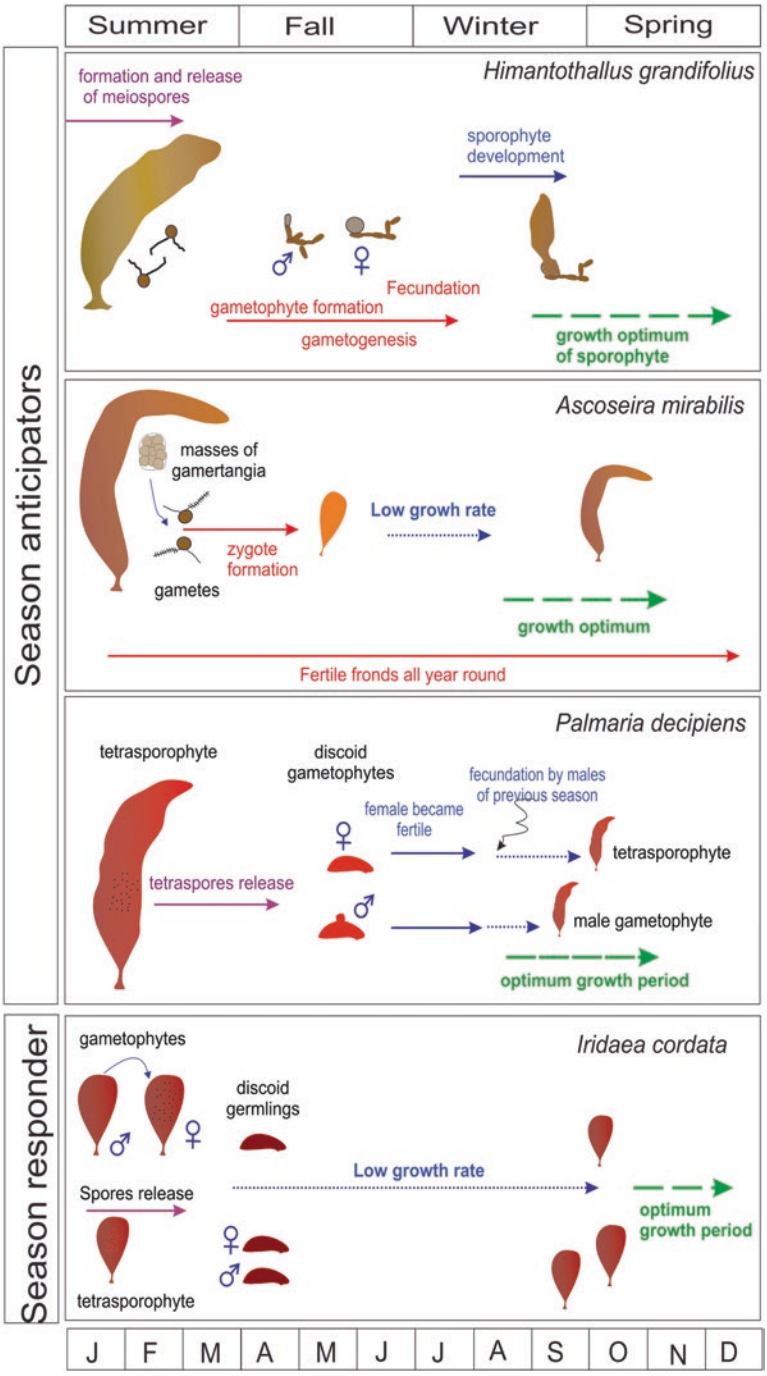

Fig. 10.1 Life history development of some conspicuous Antarctic seaweeds. The green line shows the period when growth starts. In the case of season anticipators, growth take place in late winter onwards, while in responders, growth occur during spring onwards

(Reinsch) Ricker (Wiencke 1990b), *Paraglossum salicifolia* (Reinsch) Schowe M. Lin, Fredericq, and Hommersand (formerly *Delesseria salicifolia* Reinsch), *Gymnogongrus antarcticus* Skottsberg; *G. turquetii* Hariot, *Hymenocladiopsis prolifera* (Reinsch) M. J. Wynne (formerly *H. crustigena* R.L. Moe), *Trematocarpus antarcticus* (Hariot) Fredericq and R. Moe (formerly *Kallymenia antarctica* Hariot), and *Phyllophora ahnfeltioides* Skottsberg (Dummermuth and Wiencke 2003).

Reproductive responses to the environment are particularly evident in season anticipators with strongly heteromorphic phase expression, such as in members of the genus *Desmarestia* (Wiencke et al. 1991, 1995, 1996), *Himantothallus grandifolius* (Wiencke and Clayton 1990), and *Phaeurus antarcticus* (Clayton and Wiencke 1990). The heteromorphic life history of large brown algae is characterized by the development of large perennial sporophytes and a marked reduction of the gametophytic generation (Clayton 1988). In these species, microscopic gametophytes and early stages of sporophytes grow under limited light conditions during winter, whereas adult stages of macroscopic sporophytes grow in late winter–spring (Fig. 10.1). In the case of *Desmarestia anceps*, one of the most important seaweeds in terms of biomass in the Antarctic region, the microstage of male and female gametophytes becomes fertile between July and September under a daylength of 5 and 7 h day^{-1} at photon fluence rates <3 μmol photon m^{-2} s^{-1} (Wiencke et al. 1996). The induction of fertility is a photoperiodic short-day response as revealed by the effect of a night-break regime (Wiencke 1990b; Wiencke et al. 1996), while in continuous darkness gamete formation was inhibited (Wiencke et al. 1996). Gametogenesis under short daylengths was also demonstrated in other Desmarestiales members, e.g., *Himantothallus grandifolius* (Wiencke and Clayton 1990) and *Desmarestia menziesii* (Wiencke et al. 1995; Gómez and Wiencke 1997), whereas no daylength dependence of gamete formation has been found in *Desmarestia antarctica* (Wiencke et al. 1991). In this latter species and in *Phaeurus antarcticus*, gametogenesis occurs both in short and long days. According to Wiencke et al. (2009) the phenology in these species is controlled by the sporophytic stage, which becomes fertile at daylengths between 6 and 8 h day^{-1}, while gametophytes form gametangia soon after germination (Clayton and Wiencke 1990; Wiencke 1990a; Wiencke et al. 1991). A typical feature of Antarctic Desmarestiales is the fact that they exhibit in situ fecundation, and the juvenile sporophytes remain attached to the female gametophytes (Wiencke et al. 1995, 1996). This feature could have ecological significance for the sporophytes recruitment and dominance of this group in Antarctic environment (Wiencke et al. 2006).

The brown alga *Ascoseira mirabilis,* another season anticipator, exhibits maximum growth rates in late winter–spring, while the minimum growth rates were recorded in May–June (Wiencke 1990a). However, a further, much smaller growth optimum became evident between January and March. On the other hand, unlike typical season anticipators, fertile fronds in *A. mirabilis* are present all year round, and growing and reproducing when environmental conditions are favorable (see below). *A. mirabilis* is the only member of the order Ascoseirales, and the Antarctic environmental constraints might have exerted an evolutionary pressure to develop a unique life history and reproductive biology when compared with other

Phaeophyceae (Roleda et al. 2007). The species is monoecious with sexual (isogamia) reproduction. There is one, free-living diploid generation, and zygotes develop into new individuals (Wiencke and Clayton 2002). Conceptacles are scattered all over the blades and the extrusion of gametangial masses through the ostioles precedes the release of heterokont gametes (Müller et al. 1990). Zygote formation follows immediately after fusion of gametes.

For red seaweeds, the phenology of six season anticipator species from the Antarctic, *Paraglossum salicifolium*, *Gymnogongrus antarcticus*, *Gymnogongrus turquetii*, *Hymenocladiopsis prolifera*, *Trematocarpus antarcticus*, and *Phyllophora ahnfeltioides* were investigated by Dummermuth and Wiencke (2003) in a two-year culture study under fluctuating daylengths simulating the Antarctic conditions. The period of highest growth rate in these species was registered between September and November (late winter–spring) and the formation of new blades occurred from January/February onwards. Before the summer solstice, growth ceased. However, in *Hymenocladiopsis prolifera*, the seasonal growth peak was observed in August when the light conditions increased from 3 to 25 μmol photon m^{-2} s^{-1}. This suggests that the phenology of season anticipators could not only be controlled by daylength but also by photon fluence rates. Thus, in species distributed along wide ranges of depth (e.g., 5–30 m), the seasonal growth peak could be later in the season at deeper water depths and earlier in shallower waters. Reproductive fronds were not observed, except in *Trematocarpus antarcticus,* which completed its life cycle with carpospore formation between June and August, but with the first cystocarps found in March (Dummermuth and Wiencke 2003). These results agree with the findings reported by Lamb and Zimmermann (1977), who reported cystocarps in thalli of *T. antarcticus* in January. Similarly, in *Gymnogongrus antarcticus,* cystocarps are formed in the summer (Skottsberg 1953; Cormaci et al. 1992). Cystocarps and tetrasporangia of *Paraglossum salicifolium* have been observed in late winter (Wynne 1982). Likewise, spermatangia, cystocarps, and tetrasporangia in *Delesseria sanguinea*, a comparable species in the same family, are formed during winter (Kornmann and Sahling 1977). In the case of *G. turquetii* (Kylin and Skottsberg 1919; Skottsberg 1953) and *Phyllophora ahnfeltioides* (Kylin and Skottsberg 1919), cystocarpic fronds have been reported between May and June (autumn).

The red seaweed *Palmaria decipiens*, one of the dominating species in terms of biomass, is considered as season anticipator (Wiencke 1990b; Weykam and Wiencke 1996) and displays a heteromorphic life history perfectly adapted to the Antarctic conditions. In this species female gametophytes represent the microscopic phase, while the male gametophyte develops into a macro-thallus similar in morphology to the tetrasporophytes (Fig. 10.1). The male and tetrasporophytic blades are formed in winter (Wiencke 1990b; Weykam et al. 1997) and the optimum growth period and high rates of net photosynthesis and photosynthetic efficiency coincide with increasing light intensities in spring (Wiencke 1990b; Weykam and Wiencke 1996). Tetrasporophytes become fertile in February and tetraspores develop in May into semiglobular to discoid gametophytes. The females become fertile only once from May to June. After fertilization, the female gametophyte is overgrown by the developing sporophyte, which matures and releases tetraspores in the next summer.

Interestingly, it takes about a year until male gametophytes become fertile; thus fertilization of females is only possible by mature males of the previous season, indicating a life span of the species of several years (Wiencke 1990b).

10.1.2 Season Responders

In these organisms growth and reproduction coincide with favorable light conditions in spring and summer. Thus, these species react directly to the primary factors in their environment (such as light availability) and show an opportunistic life strategy (Wiencke 1990a, b). Most of the season responder species are distributed in the eulittoral and upper sublittoral zone, and they can have temperate or cold-temperate affinities (Wiencke et al. 2007; Navarro et al. 2019; see Chap. 12 by Campana et al.). Well-known members of this group are the red seaweeds *Iridaea cordata* (Turner) Bory (Weykam et al. 1997) and *Gigartina skottsbergii* Setchell *et* N.L. Gardner (Wiencke 1990b), the brown alga *Adenocystis utricularis* (Bory) Skottsberg (Wiencke 1990a), and the green seaweeds *Ulva hookeriana* (Kützing) H. S. Hayden, Blomster, Maggs, P. C. Silva, Stanhope, and Walland (formerly *Enteromorpha bulbosa* (Suhr) Montagne and *Acrosiphonia arcta* (Dillwyn) J. Agardh (Wiencke 1990b).

The pseudoperennial *Gigartina skottsbergii* and *Iridaea cordata* have a triphasic life history with isomorphic haploid male and female gametophytes and a diploid tetrasporophyte. They occur normally in eulittoral pools and in the upper sublittoral, but also can be found down to 30 m (Wiencke and Clayton 2002; Navarro et al. 2016). Both species show the maximum growth rate during the spring-summer season (e.g., December), while the minimum growth rates were recorded from May to July (Wiencke 1990b). Mature tetrasporophytes and gametophytes of *Iridaea cordata* were observed during spring-summer (Roleda et al. 2008; Navarro et al. 2016). Tetraspores and carpospores of this species germinate normally forming a discoid germling from which new plantlets arise from July onwards. The plantlets show a growth optimum between September and November and large blades are formed in summer (Wiencke 1990b). Regrowth from the perennial basal parts of the blades is possible (Wiencke and Clayton 2002), which could explain its dominance at the eulittoral (Marcías et al. 2017). In the case of *G. skottsbergii*, Wiencke (1990b) reported the induction of sporangium formation in tetrasporophytes in the laboratory by the end of September, when irradiances were between 27 and 46 μmol photon m^{-2} s^{-1}, but spores were not released before June. In contrast, in the field, reproductive fronds with viable propagules have been collected in October (Roleda et al. 2008) and January (Navarro et al. 2016). This discrepancy in reproductive periods might be related to differences related to the experimental setup of laboratory cultures by Wiencke (1990b). As suggested for the season anticipator *Hymenocladiopsis prolifera*, photon fluence rates might also control the seasonal phenology of this species. Thus, these algae apparently have the capacity to reproduce during a prolonged time span under changing environmental conditions.

Adenocystis utricularis has a heteromorphic life cycle with a sporophytic macrothallus and gametophytic microthallus. Spores from the macrothalli develop into microscopic filamentous, dioecious gametophytes (Wiencke and Clayton 2002), the dominant life phase under winter conditions in laboratory culture (Wiencke 1990a). Macrothalli start to develop asexually on crustose parts of the microthalli from June onwards. Between October and December, growth rates of macrothalli are optimal. Reproductive macrothalli are present in January–February, while release of spores occurs in February, after which the thalli disintegrate.

As suggested for other species with heteromorphic phase expression, the microthallus is probably an important over-wintering stage (Wiencke and Clayton 2002). However, eventually all developmental stages can be present at the same time depending where they occur. De Reviers and Délépine (1981) reported that macrothalli are present throughout the year with juveniles being most abundant in October in the eulittoral zone, while in the sublittoral zone, small macrothalli are present only from November to June. Laboratory experiments where the photon fluence rates varied from 2 to 46 μmol photon m^{-2} s^{-1} confirmed this field observation (Wiencke 1990a). Thus, in the eulittoral zone, *A. utricularis* occurs as an aseasonal annual, while in upper sublittoral zone, the species probably occurs as a seasonal annual due to less available light. The species has been reported to occur down to 20 m (Wiencke and Clayton 2002), and at these depths the alga possibly is biannual as suggested by Wiencke (1990a).

10.2 Photosynthetic Light Requirements of Early Stages

Irrespective of the life history strategy, the Antarctic environment imposes physiological constraints to the reproductive output (propagules), settlement, recruitment, and growth of seaweeds. However, seaweeds have adapted their biological processes by evolving different functional mechanisms to cope with the Antarctic light and temperature conditions. In general, Antarctic seaweeds are very low light adapted, adult phases being able to photosynthesize at irradiances as low as 10 μmol photon m^{-2} s^{-1}, while propagules can photosynthesize at even lower irradiances (Gómez et al. 2009). In Table 10.1 the saturating irradiances of photosynthesis (E_k values) of different Antarctic seaweed propagules are summarized, and in Fig. 10.2 mean values of E_k for propagules from eulittoral and sublittoral algae are plotted. With the exception of some eulittoral species, most of the studied Antarctic seaweeds exhibit E_k values lower than 60 (μmol photon m^{-2} s^{-1}). Although differences in saturation irradiance between eulittoral (65 ± 20 μmol photon m^{-2} s^{-1}) and sublittoral (40 ± 15 μmol photon m^{-2} s^{-1}) exist, propagules are able to adapt to different light conditions (quantity and quality) mainly during the winter–spring transition. This is particularly evident in propagules of species that colonize a wide range of vertical distribution (e.g., *Desmarestia anceps*). After sea ice breakup in King George Island (South Shetland Islands), light can penetrate down to 30 m

Table 10.1 Overview of light requirement for saturation (E_k), photosynthetic efficiency (α_{ETR}), inhibition by PAR and PAR + UV radiation, and subsequent recovery in different life history stages of Antarctic seaweeds collected from different depths. Propagule size and date of collection are also indicated. Irradiance values represent conditions during incubation in the laboratory. PAR and PAR + UV inhibition were calculated after 4 h of exposition according to information provided in the papers)

Species	Depth	Date of collection	Cell diameter (μm)	Irradiance (μmol m^{-2} s^{-1})	E_k	α_{ETR}	F_v/F_m	PAR inhibition	PAR + UV inhibition	Recovery	Reference
Urospora penicilliformis zoospores, gametes	Upper eulittoral (0 m)	Oct 2004	6	22	87	0.16	~0.50	No	~37% (PA; 4 h); ~39% (PAB; 4 h)	100% (24 h)	Roleda et al. (2009)
Urospora penicilliformis gametophytes	Upper eulittoral (0 m)	Oct 2004		22	252	0.18	~0.51	No	~20% (PA; 4 h); ~23% (PAB; 4 h)	94% (1 h)	Roleda et al. (2009)
Pyropia endiviifolia carpospores	Eulittoral (0 m)	Jan–Feb 2015	12 ± 1	13	101 ± 19	0.14 ± 0.01	0.35 ± 0.01	No	~16% (PAB, 4 h)	100% (4 h)	Navarro et al. (2016, 2019)
Pyropia endiviifolia monospores	Upper eulittoral (0 m)	Jan–Mar 2005	15 ± 2	23	33	0.12	0.49 ± 0.04	46% (4 h)	~56% (PA; 4 h); ~60% (PAB; 4 h);	100% (48 h)	Zacher et al. (2007)
Adenocystis utricularis zoospores	Eulittoral (0–1 m)	Jan–Feb 2015	6 ± 1	13	59 ± 6	0.45 ± 0.01	0.64 ± 0.02	No	~2% (PAB, 4 h)	100% (4 h)	Navarro et al. (2016)
Adenocystis utricularis zoospores	Eulittoral (0–1 m)	Jan–Mar 2005	4	23	64	0.14	0.46 ± 0.11	No	~20% (PA; 4 h); ~57% (PAB; 4 h);	100% (48 h)	Zacher et al. (2007)

Monostroma hariotii gametes	Eulittoral (0–1 m)	Jan–Feb 2015	5 ± 0.5	13	295 ± 84	0.09 ± 0.01	0.26 ± 0.01	23% (4 h)	~28% (PAB; 4 h)	100% (4 h)	Navarro et al. (2016, 2019)
Monostroma hariotii gametes	Eulittoral (0 m)	Jan–Mar 2005	7	23	83	0.065	0.29 ± 0.04	50% (4 h)	~66% (PA; 4 h); ~71% (PAB; 4 h);	100% (48 h)	Zacher et al. (2007)
Iridaea cordata tetraspores	Eulittoral (0–1 m)	Jan–Feb 2015	18 ± 2	13	46 ± 6	0.17 ± 0.03	0.39 ± 0.06	No	~20% (PAB; 4 h)	100% (4 h)	Navarro et al. (2016, 2019)
Iridaea cordata tetraspores	Upper sublittoral (0 m)	Oct 2004	20 ± 2	22	57	0.12	0.47 ± 0.04	53% (4 h)	~78% (PA; 4 h); ~82% (PAB; 4 h)	100% (2 d)	Zacher et al. (2009)
Gigartina skottsbergii carpospores	Sublittoral (5–8 m)	Jan–Feb 2015	25 ± 2	13	27 ± 9	0.27 ± 0.05	0.42 ± 0.32	52% (4 h)	~80% (PAB, 4 h)	35–60% (4 h)	Navarro et al. (2016)
Gigartina skottsbergii carpospores	Sublittoral (3 m)	Oct 2004	27 ± 2	22	54 ± 2	0.14	0.40 ± 0.03	73%	~87% (PA; 4 h);89% (PAB; 4 h)	100% (2 d)	Roleda et al. (2008)
Gigartina skottsbergii tetraspores	Sublittoral (3 m)	Oct 2004	23 ± 1.5	22	44 ± 21	0.14	0.31 ± 0.07	69% (4 h)	~86% (PA; 4 h);90% (PAB; 4 h)	100% (2 d)	Roleda et al. (2008)
Ascoseira mirabilis gametangia	Deep sublittoral (17–30 m)	Jan–Feb 2015	22 ± 4	13	17 ± 5	0.21 ± 0.03	0.48 ± 0.02	16% (4 h)	~30% (PAB; 4 h)	85% (4 h)	Navarro et al. (2016)

(continued)

Table 10.1 (continued)

Species	Depth	Date of collection	Cell diameter (μm)	Irradiance (μmol m^{-2} s^{-1})	E_k	α_{ETR}	F_v/F_m	PAR inhibition	PAR + UV inhibition	Recovery	Reference
Ascoseira mirabilis gametangia	Upper sublittoral (2 m)	Oct 2004	8–10	22	52	0.09	0.40 ± 0.06	85% (4 h)	~91% (PA; 4 h); 95% (PAB; 4 h)	100% (2 d)	Roleda et al. (2007)
Ascoseira mirabilis conceptacles	Shallow sublittoral (1 m)	Jan 2014		13	52 ± 14	0.20 ± 0.04	~0.6		~0% (6 h)	100% (14 h)	Huovinen and Gómez (2015)
Cystosphaera jacquinotii receptacles	Deep sublittoral	Jan–Feb 2015		13	13 ± 6	0.28 ± 0.01			~15–21% (2 h)	~ 90% (4 h)	Huovinen and Gómez (2015)

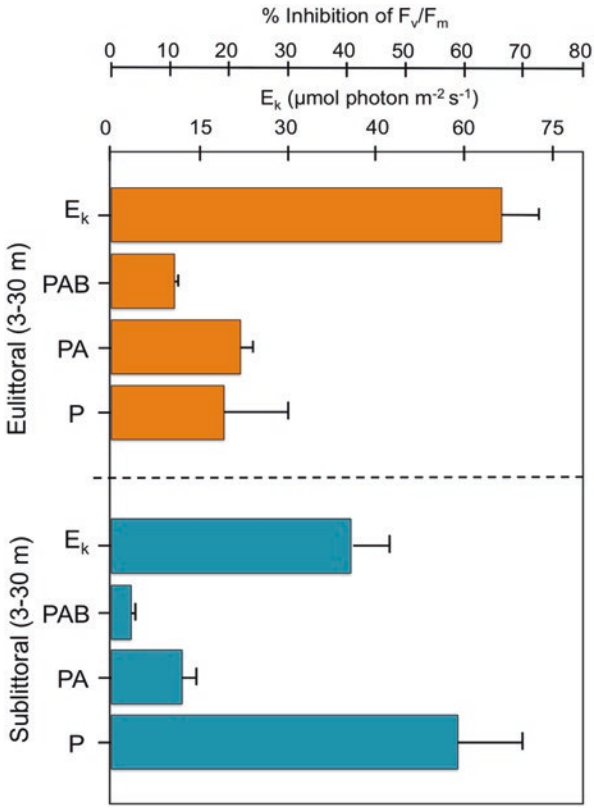

Fig. 10.2 Summary of light requirement for saturation (E_k) and inhibition by PAR and PAR + UV radiation in propagules of eulittoral and sublittoral Antarctic seaweeds. PAR and PAR + UV inhibition were calculated after 4-h exposure according to the information provided in each of the studies consulted. For references, see Table 10.1

depth reaching an average of photon fluence rates of 70 µmol photon m^{-2} s^{-1} (Gómez et al. 1997). This level of irradiance can also be strongly attenuated in terms of spectral characteristics under the canopy of large brown algae (Huovinen et al. 2016; Gómez et al. 2019). Below the canopy the spectrum is enriched in green and in far red light, probably affecting photosynthesis as well as the photomorphogenetic development of the understory species (Salles et al. 1996) (see Chap. 7 by Huovinen and Gómez).

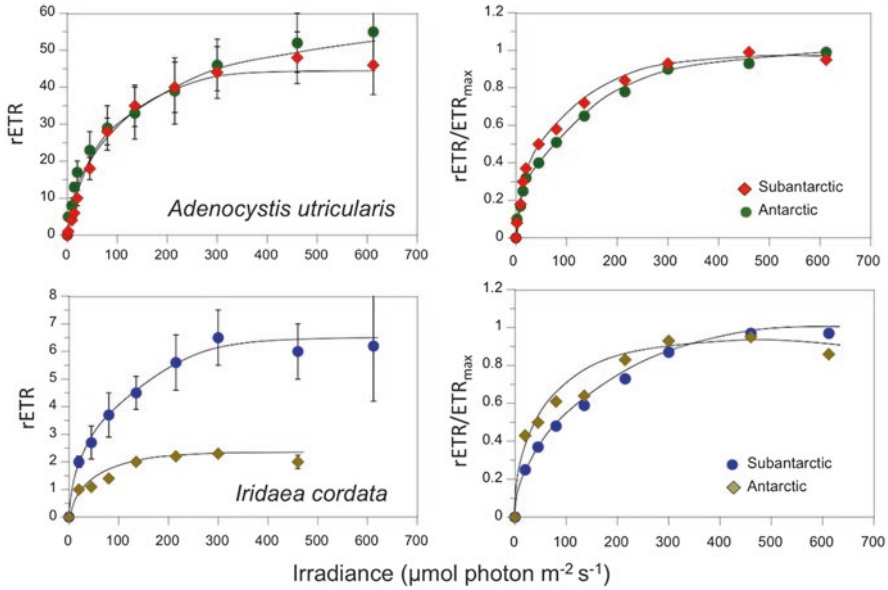

Fig. 10.3 Rapid light curves (PAR vs rETR) and rETR/ $rETR_{max}$ ratio of Antarctic and sub-Antarctic populations of *Adenocystis utricularis* and *Iridaea cordata* measured using chlorophyll fluorescence. $rETR_{max}$ represents the maximum value for each curve. (Modified from Navarro et al. 2019)

10.2.1 Estimating Photosynthetic Parameters from Chlorophyll Fluorescence

Photosynthetic characteristics of propagules of Antarctic seaweeds are normally determined estimating photosynthetic parameters (ETR_{max}, alpha and saturation irradiance, E_k) calculated from P-E curves (summarized in Gómez et al. 2009). When P-E curves are based on chlorophyll fluorescence measurements, the electron transport rates (ETR) are commonly used as a parameter (Fig. 10.3). Considering the limitations of the fluorescence method, as well as various factors that can affect light requirements, e.g., form, season, size, number of cells, chlorophyll concentration, etc., the P-E curve-derived light requirements for photosynthesis (E_k) represent the best measures to estimate shade adaptation in adult (Huovinen and Gómez 2013) and early stages (Zacher et al. 2007; Roleda et al. 2008, 2009; Navarro et al. 2016, 2019). However, two important aspects for calculation of electron transport rates are sometimes not considered: (1) the proportional rates of chlorophyll *a* at each photosystem (FII factor), which is different between red, green, and brown algae (Grzymski et al. 1997), and (2) the amount of light absorbed by the algal samples (absorptance). Due to the difficulty of measuring absorptance in a propagule suspension, the use of the relative ETR has been proposed (Beer et al. 2001). This parameter provides useful information for the description of relative changes

in photosynthetic activity if the experimental approach uses standardized measurements.

Thus, the comparison of photosynthetic parameters of propagules using the ETR-based P-E curves must be made with caution. Alternatively, the rETR can be normalized to $rETR_{max}$ (with $rETR_{max}$ as the maximum value for each curve) expressing the rETR curve between 0 and 1 (relative units), which allows comparing propagules from species with very different ETR values. For example, Navarro et al. (2019) showed differences in photosynthetic performance of propagules from congeneric and conspecific Antarctic/sub-Antarctic seaweeds using the rETR and $rETR/rETR_{max}$ ratio curves. While the rETR curve demonstrates that tetraspores of *I. cordata* from Antarctic populations exhibit very low rETR values when compared to the sub-Antarctic population, the $rETR/rETR_{max}$ ratio allows detecting differences in the shape of the curves (Fig. 10.3).

10.3 Effects of Environmental Factors on the Biology of Propagules

10.3.1 High Solar Radiation

Environmental shifts will affect recruitment, and consequently, the whole fate of the seaweed population and their maintenance through time. Once Antarctic seaweed spores or gametes are released, they face a completely different physical environment than what existed when they were housed in the parental reproductive structures (Amsler et al. 1992; Zacher 2014). During the last decade, various studies have examined the effects of stress factors (e.g., temperature and UV radiation) on microscopic stages, e.g., propagules and plantlets, of some selected Antarctic seaweeds (Gómez et al. 2009; Roleda et al. 2009; Zacher et al. 2009; Navarro et al. 2016). There is a consensus that propagules are the most susceptible life stage of seaweeds in terms of their responses to environmental perturbations. However, the effect of a given factor on the propagule physiology is highly variable, depending on a suite of environmental and endogenous factors, which can act synergistically or antagonistically.

It is well known that UV wavelengths cause direct and indirect effects on algal cells (e.g., Karsten et al. 2009). The direct effects are normally mediated by absorption of UV by important biomolecules, in particular the DNA, enzymes, and membrane components (Vass 1997). In the case of propagules, which attain small size, translucent cytosol and an incipient development of the cell wall, UV radiation can easily reach the DNA where diverse injuries are produced, e.g., formation of cyclobutane pyrimidine dimers (CPDs) (Wiencke et al. 2000). This results in the inability of RNA and DNA polymerases to recognize the damaged sectors, causing the interruption of gene transcription and DNA replication (Britt 1995).

Consequently, modifications in the metabolism, cellular division, and germination of unicellular propagules can occur (Huovinen et al. 2000).

DNA damage has been reported in propagules of eulittoral Antarctic seaweeds *Adenocystis utricularis*, *Monostroma hariotii*, and *Iridaea cordata* after exposure to different doses of UV radiation (Roleda et al. 2007, 2008; Zacher et al. 2007, 2009). In general, the amount of CPDs increases with increasing UV-B dose; however, lesions can be effectively repaired after 48 h under photoreactivation processes (Zacher et al. 2007, 2009). Besides, contrasting patterns have been detected in species from different depths: propagules of *Pyropia endiviifolia* from upper eulittoral did not exhibit CPDs under different UV-B doses (Zacher et al. 2007), while propagules of *Gigartina skottsbergii* and *Ascoseira mirabilis* from the deep sublittoral were more affected and not able to repair their damaged DNA completely after 8-h UV-B exposure (0.4 Wm^{-2}) (Roleda et al. 2007, 2008). Interestingly, in the case of *Gigartina skottsbergii,* the accumulation of DNA damage was related to the ploidy level of the propagules: DNA damage was lower in diploid carpospores ($2n$) compared to haploid tetraspores (n) suggesting that diploid carpospores are more tolerant to UV radiation in terms of UV-B-induced DNA damage (Roleda et al. 2008). These authors suggested that higher UV-stress tolerance of diploid carpospores than haploid tetraspores could be related to the genetic buffering hypothesis, which says that diploid organisms are more vigorous and tolerant to stress than haploid ones, i.e., the two copies of every gen confer them advantages to withstand the effects of deleterious recessive mutations (Raper and Flexer 1970; Gerstein et al. 2010). However, diverse studies have stated many important genetic advantages of haploidy such as lower mutation load and more rapid spread of beneficial alleles and of diploidy, e.g., protection from somatic mutation and heterozygote advantage (Otto and Gerstein 2008). In fact, in spite of the higher DNA damage, tetraspores of *G. skottsbergii* exhibited a higher DNA damage repair rate than carpospores when the UVR was excluded. It must be noted that DNA damage in spores exposed to high UV-B dose was not repaired completely after 2 days of post-cultivation, and the remaining DNA damage was lower in carpospores than in tetraspores (Roleda et al. 2008).

UV radiation affects also photochemical processes, especially inhibiting the energy transfer within the PSII reaction center by blocking the electron flow. UV-B radiation affects the D1/D2 protein complex (Richter et al. 1990) mainly by fragmenting the D1 protein (Vass 1997; Bischof et al. 2006) through UV-active chromophores on both the donor and acceptor side of this protein (Bouchard et al. 2006). On the oxidizing side, the oxygen evolving system (water splitting complex) is another sensitive target of UV-B (Renger et al. 1986). Moreover, it has been suggested that UV-B can affect the antenna complex through the functional shutdown of the photosystem, resulting in a failure in the transfer of energy to the reaction center (Renger et al. 1986; Lorenz et al. 1997; Bischof et al. 2006). In propagules of Antarctic seaweeds, UV radiation has also been pointed out as responsible for the decrease in photosynthetic activity, measured as decreases in optimum quantum yield-F_v/F_m. For example, Navarro et al. (2016) reported that propagules of species from the eulittoral (e.g., *Iridaea cordata*, *Pyropia endiviifolia*, *Adenocystis*

utricularis) showed <20% inhibition in F_v/F_m from UV (1.5 and 0.26 Wm^{-2} of UV-A and UV-B, respectively) after 4 h of exposure, while propagules of the red alga *G. skottsbergii* collected in the sublittoral were more sensitive exceeding 30% inhibition in F_v/F_m in the same condition. It is important to emphasize, however, that photochemical reactions of propagules from Antarctic seaweeds can also be strongly photoinhibited by PAR (Fig. 10.2). For example, 1-h exposure under 22 μmol photons m^{-2} s^{-1} of PAR decreased F_v/F_m in propagules of the sublittoral *G. skottsbergii* (53–58%) (Roleda et al. 2008) and *A. mirabilis* (62%) (Roleda et al. 2007) and in the eulittoral *M. hariotii* (62%), *P. endiviifolia* (81%) (Zacher et al. 2007), and *I. cordata* (~25%) (Zacher et al. 2009). Increasing exposure time further reduced F_v/F_m in all these species, with exception of *M. hariotii* (Zacher et al. 2007). In contrast, in the case of propagules of the eulittoral *Adenocystis utricularis* (Zacher et al. 2007) and *Urospora penicilliformis* (Roleda et al. 2009), the photosynthetic activity was not affected by PAR. PAR supplemented with UV-A (~4.3 Wm^{-2}) decreased photosynthetic efficiency significantly compared to only PAR treatment in all mentioned species during 1-h exposure. However, additional UV-B (~0.35 Wm^{-2}) revealed a further decrease of F_v/F_m only in sublittoral *Ascoseira mirabilis* (25%) and *G. skottsbergii* (3–7%) (Roleda et al. 2007, 2008). Although UV radiation further decreased photosynthetic efficiency in these species, all propagules recovered completely after 48 h (Table 10.1).

Additionally, the UV susceptibility has been related to propagule size as cell path length affects various bio-optical processes such as scattering and spectral extinction (Swanson and Druehl 2000; Roleda et al. 2008; Navarro et al. 2016). However, at the cellular level, UV tolerance does not seem to respond to complex biochemical and bio-optical processes. For example, tetraspores of *I. cordata* from Antarctica exhibit a smaller size but very high UV tolerance compared to tetraspores of the same species from sub-Antarctic region (Navarro et al. 2019). UV tolerance can also be related to the presence and/or the capacity to induce formation of UV-absorbing compounds, what could result in a more effective UV photoprotection, still in small propagules (Roleda et al. 2008). To our knowledge, only few studies have described absorption of UV in Antarctic seaweed propagules under UV stress. Higher concentration of palythine (λ_{max} = 320 nm) than shinorine (λ_{max} = 334 nm) has been reported in freshly released tetraspores of *G. skottsbergii* (Roleda et al. 2008) and *I. cordata* (Zacher et al. 2009). However, contrasting patterns in MAA content were observed after 8 h under PAR or PAR + UV treatments, while the total content of MAAs in tetraspores of *G. skottsbergii* was not significantly different between control (freshly released spores) and treatment. In contrast, MAA concentration in spores of *I. cordata* decreased in treated compared to freshly released spores. Based on these findings, it could be suggested that (1) freshly released propagules could have a basal level of UV-absorbing substances due to the higher in situ incident solar radiation in the field and (2) the level of UV-absorbing substances can acclimate depending on environmental conditions. In the first case, the synthesis of UV-absorbing substances would take place when the spores are still protected by the thick tissue of the parental thalli (tetrasporangial tissue in the case

of tetraspores of *G. skottsbergii* and *I. cordata*). For *I. cordata*, Karsten et al. (2000) reported a higher amount of MAAs in tetrasporangial tissue than in vegetative parts of the thalli. Similarly, Huovinen and Gómez (2015) reported that reproductive tissue of *Ascoseira mirabilis* and *Cystosphaera jacquinotii* contain higher amounts of soluble phlorotannins, a type of UV-absorbing phenols found in brown algae. The presence of these compounds in reproductive tissues could ensure the maturation, survival, and germination of released propagules when they are exposed to UV radiation in the water column. Although photoprotection was only partial in laboratory experiments, propagules of *I. cordata* and *G. skottsbergii* tetraspores exposed to UV-B radiation showed the higher total MAAs in comparison with those incubated under only PAR (Roleda et al. 2008; Zacher et al. 2009).

10.3.2 Temperature

Antarctic seaweed propagules are adapted to low temperature. Cold adaptation was confirmed by the high photosynthetic efficiency (in terms of maximum quantum yield of fluorescence – F_v/F_m) at 0 °C in six Antarctic distributed species (Navarro et al. 2016). This low temperature requirement for photosynthesis is certainly the result of the long Antarctic cold-water history of at least 14 Ma (Crame 1993). However, it is well known that photosynthesis increases progressively with increasing temperature and then rapidly declines near upper critical temperature (Davison 1991). In the case of Antarctic species, the optimum temperature for photosynthesis is between 10 and 20 °C (Eggert and Wiencke 2000; Eggert 2012), lower than that reported for algae from other geographic regions (reviewed in Gómez et al. 2009). In propagules of eulittoral species such as *Adenocystis utricularis*, *Monostroma hariotii*, and *Pyropia endiviifolia* and shallow sublittoral *Ascoseira mirabilis*, the highest photosynthetic efficiency was observed at 25 °C (Navarro et al. 2016). This suggests that propagules of these species are thermally well adapted (eurythermal species), allowing them to develop in a highly variable environment or in different biogeographic regions. For example, *A. utricularis* and *M. hariotii* are widely distributed in sub-Antarctic and temperate coasts of South America (Huovinen and Gómez 2012, see Chap. 2 by Oliveira et al. and Chap. 4 Macaya et al.). In contrast, the high photosynthetic efficiency exhibited by propagules of Antarctic endemic *Ascoseira mirabilis* at 25 °C could be explained by the upper vertical distribution of the parental sporophytes or could be a conserved trait related to the fact that the species is probably a relic of Mesozoic (Gondwana) marine flora, which was highly diverse when the average water temperatures were close to 12 °C (Clayton 1994).

Temperature is a factor modifying the susceptibility/tolerance to UV radiation. The influence of this factor apparently depends on the position of parental thalli on the shore. In this context, a recent study provided evidence that propagules of Antarctic seaweeds are relatively tolerant to enhanced temperature, which can furthermore modulate UV tolerance at least under laboratory conditions (Navarro et al.

2016). These authors observed that the exposure of propagules to a combination of UV radiation and temperature stress inhibits the photosynthetic capacity of propagules of six Antarctic seaweed species from the eulittoral (*Pyropia endiviifolia*, *Iridaea cordata*, *Adenocystis utricularis*, and *Monostroma hariotii*) and the sublittoral (*Ascoseira mirabilis,* and *Gigartina skottsbergii*), the former group being more tolerant to UV and enhanced temperature than the sublittoral group. Additionally, propagules of eulittoral species *P. endiviifolia*, *I. cordata,* and *A. utricularis* exhibit negative UV effects at 2 °C compared to 7 and 12 °C, suggesting that enhanced temperature improves UV tolerance. On the contrary, this positive interaction was not observed in propagules of the shallow sublittoral *A. mirabilis*, where an increase in temperature exacerbates the reduction of photosynthetic efficiency (Navarro et al. 2016). It is known that various processes related to photoprotection, e.g., D1 protein turnover, enzyme repair mechanisms, and dissipative quenching, operate more efficiently at higher temperatures (Wünschmann and Brand 1992; Becker et al. 2010). Thus, the lower inhibition of photosynthesis observed at 12 °C compared to 2 and 7 °C can be regarded as an efficient acclimation of photosynthesis in these cells. Even though photosynthesis was inhibited by UV radiation, propagules from eulittoral species recover completely after 4 h under dim visible light, whereas sublittoral ones do not. A fast turnover of D1 protein may be responsible for the fast reversible photoinhibition of photosynthesis in eulittoral macroalgae as suggested for *Urospora penicilliformis* propagules (Roleda et al. 2009). However, the recovery is not influenced by a temperature increase in the studied species (Navarro et al. 2019).

Antarctic propagules can retain their capacity to tolerate elevated temperatures, which is evident when they are compared with their sub-Antarctic counterparts. For example, F_v/F_m measured in *I. cordata* tetraspores from Antarctica was not inhibited by UV radiation at 2 °C or 8 °C, while propagules from sub-Antarctic populations exhibited a decrease after a 4-h exposure, mainly at 2 °C in PAR (30%) and PAR + UV (67%). Considering only the effects of temperature, F_v/F_m decreased by 14% in tetraspores from sub-Antarctic population exposed at 2 °C when compared to the control (8 °C). Surprisingly, photosynthetic activity in tetraspores from Antarctic increased by 2% relative to control. These results suggest that low temperatures may exacerbate UV stress to photosynthesis in spores from the sub-Antarctic population, whereas Antarctic spores would be adapted to low temperature and UV. The results also confirm previous evidence obtained in adult thalli of *Ulva* spp. from Antarctic and sub-Antarctic region by Rautenberger and Bischof (2006). At 10 °C the inhibition of *Ulva hookeriana* (known as *Enteromorpha bulbosa* (Suhr) Montagne) from Antarctica was comparable to its sub-Antarctic counterpart *Ulva clathrata* (10% of control). However, at 0 °C, inhibition was of 50% in the sub-Antarctic *Ulva clathrata* and 37% in *U. hookeriana* (Rautenberger and Bischof 2006). Overall, the results indicate that in cold-adapted species, stress tolerance can be efficient, which allow many shallow sublittoral, and especially eulittoral species, to thrive under extremely changing thermal conditions.

10.3.3 Other Environmental Stressors

In the Antarctic environment, seaweeds are also facing fluctuations of other environmental factors such as salinity, influenced by local meltwater influx and calving glaciers as well as desiccation when algae are exposed to air during low tides. Although the effects of salinity on seaweeds are relatively well known (reviewed in Kirst 1990 and Karsten 2012), few studies have been conducted on Antarctic seaweeds (e.g., Jacob et al. 1991, 1992a, b; Karsten et al. 1991a, b). In general, it has been reported that seaweeds respond to external salinity changes with osmotic acclimation processes involving the control of internal organic (e.g., proline, sucrose, β-dimethylsulphoniopropionate) and inorganic (K^+, Na^+, Mg^{2+}, Cl^-, SO_4^{2-}, and PO_4^{3-}) ions (Karsten et al. 1991a, b; Kirst 1990). Antarctic seaweeds inhabiting the eulittoral and supralittoral zone can be characterized as euryhaline organisms, which can survive salinities between 7 and 102 PSU with a low rate of mortality. Most taxa grow, photosynthesize, and respire optimally under normal seawater conditions with rather broad tolerances between 7 and 68 PSU. Hitherto, there is no information of the effect of salinity on Antarctic seaweed propagules. On the other hand, emergent stressors in Antarctic environment, e.g., ocean acidification (Hurd et al. 2009) and marine pollution (Goutte et al. 2013), can pose risks to adult and early phases of Antarctic seaweeds. Ocean acidification can affect the physiology of seaweeds; however, practically no data exist on their effects on early phases of macroalgae. In the giant kelp *Macrocystis pyrifera*, pH between 7.59 and 7.60 reduced meiospore germination, which was ameliorated when CO_2 was added (Roleda et al. 2011). Hitherto there is no information on the effects of these compounds on the biology of Antarctic propagules.

It has been suggested that metals may inhibit reproduction in brown algae by interfering with the ability of sperm to find eggs, perhaps via interference of the pheromone attractant (Maier 1993). However, the effect of trace metals is expected to be detrimental to propagules (spores, gametes, and zygotes) due to poor development of the protective cell wall. Moreover, cell walls of brown seaweeds composed of alginate and fucoidan can bind cations and have a high affinity for copper (Lignell et al. 1982), affecting the settlement and germination of propagules. For example, in *Lessonia*, copper drastically affected spore release by mature sporophytes as well as spore settlement. The highest copper concentration applied interrupted the development of the spores totally after settlement (Contreras et al. 2007). In all, the importance of studying the effects of metals and other pollutants (hydrocarbons, pesticides, other persistent pollutants, and so on) on Antarctic algae propagules lies in the recent increase of contaminant concentration in Antarctic due to human activities (Bargagli 2008). On the other hand, although the harmful effects of metals, e.g., copper toxicity, have been analyzed in brown species (reviewed by Coelho et al. 2000; Contreras et al. 2007), the effects of these new, emergent stressors on the biology of Antarctic seaweeds have to be examined in a context of the combined action of multiple factors (see Chap. 7 by Huovinen and Gómez).

10.4 Concluding Remarks: Biology of Propagules under Climate Change

Despite having a crucial importance in the biology of seaweeds, propagules have not been sufficiently studied in relation to their physiological requisites to respond to climate change. The importance of understanding the effects of global climate change on reproductive stages lies in the fact that early stages of development are essential for recruitment, especially for those species that rely their dominance entirely on reproductive abilities.

The predicted increase of temperature and the prevalence of episodes of depleted ozone around the Antarctic Peninsula region and adjacent islands will impose physiological constraints to reproductive output, settlement, and recruitment of different species of seaweeds. Increase in seawater temperature could also influence the phenology and the formation of propagules (spores and/or gametes) and consequently, the timing and formation of juvenile thalli, especially in species inhabiting the eulittoral and shallow sublittoral zone (Zacher et al. 2007; Campana et al. 2009; see Chap. 12 by Campana et al.). Furthermore, as a consequence of temperature increase, glaciers can retreat opening new free space for recruitment of benthic organisms, including macroalgae (Quartino et al. 2013; see Chap. 8 by Quartino et al.). In these new open areas, however, alteration in light, salinity, sedimentation, and disturbance processes can occur, limiting settlement of established communities and even favoring the arrival of cold-temperate species (see also Chap. 9 by Deregibus et al.). Increased turbidity can have, however, contrasting implications for the biology of reproductive cells, which can become favored by a minimized impact of UV radiation, but decreasing available irradiance for photosynthesis.

Undoubtedly, Antarctic seaweeds have developed life strategies to colonize and form a complex structure in the coastal ecosystems. In scenarios of climate change and warming in the Antarctic, dispersal and colonization of Antarctic coastal zones via efficient adaptations of early developmental phases of seaweeds are central to envision the future seaweed diversity in Antarctica (see Chap. 2 by Oliveira et al. and Chap. 5 by Pellizzari et al.).

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References

Amsler C, Reed D, Neushul M (1992) The microclimate inhabited by macroalgal propagules. Eur J Phycol 27:253–270

Bargagli R (2008) Environmental contamination in Antarctic ecosystems. Sci Total Environ 400:2012–2226

Becker S, Graeve M, Bischof K (2010) Photosynthesis and lipid composition in the Antarctic rhodophyte *Palmaria decipiens*: effects of changing light and temperature levels. Polar Biol 33:945–955

Beer S, Björk M, Gademan R, Ralph P (2001) Measurements of photosynthesis rate in seagrass. In: Short FT, Cole R (eds) Global seagrass research methods. Elsevier Publishing, Amsterdam, pp 183–198

Bischof K, Gómez J, Molis M et al (2006) UV radiation shapes seaweed communities. Rev Environ Sci Biotechnol 5:141–166

Bouchard JN, Roy S, Campbell DA (2006) UVB effects on the photosystem II-D1 protein of phytoplankton and natural phytoplankton communities. Photochem Photobiol 82:936–951

Britt AB (1995) DNA damage and repair in plants. Annu Rev Plant Physiol Plant Mol Biol 47:75–100

Campana GL, Zacher K, Fricke A et al (2009) Drivers of radiation colonization and succession in polar benthic macro- and microalgal communities. Bot Mar 52:655–667

Clayton MN (1988) Evolution and life histories of brown algae. Bot Mar 31:379–387

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

Clayton MN, Wiencke C (1990) The anatomy, life history and development of the Antarctic brown alga *Phaeurus antarcticus* (Desmarestiales, Phaeophyceae). Phycologia 29:303–315

Coelho SM, Rijstenbil JW, Brown MT (2000) Impacts of anthropogenic stresses on the early development stages of seaweeds. J Aquat Ecosyst Stress Recover 7:317–333

Contreras L, Medina MH, Andrade S et al (2007) Effects of copper on early developmental stages of *Lessonia nigrescens* Bory (Phaeophyceae). Environ Pollut 145:75–83

Cormaci M, Furnari G, Scammacca B (1992) The benthic alga flora of Terra Nova Bay (Ross Sea, Antarctica). Bot Mar 35:541–552

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

Davison IR (1991) Environmental effects on algal photosynthesis: temperature. J Phycol 27:2–8

de Reviers B, Délépine R (1981) Biological data on a southern Phaeophyceae *Adenocystis utricularis* (Bory) Skottsberg, possible material for alginate industry. Proc 10th Int Seaweed Symp, p 345–350

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

Eggert A (2012) Seaweed responses to temperature. In: Wiencke C, Bischof K (eds) Seaweed biology: novel insights into ecophysiology, ecology and utilization. Ecological studies, vol 219. Springer, Berlin, pp 47–66

Eggert A, Wiencke C (2000) Adaptation and acclimation of growth and photosynthesis of five Antarctic red algae to low temperatures. Polar Biol 23:609–618. https://doi.org/10.1007/s003000000130

Gerstein AC, Cleathero LA, Mandegar MA, Otto SP (2010) Haploids adapt faster than diploids across a range of environments. J Evol Biol 24:531–540

Gómez I, Wiencke C (1996) Photosynthesis, dark respiration and pigment contents of gametophytes and sporophytes of the Antarctic brown alga *Desmarestia menziesii*. Bot Mar 39:149–157

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

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, 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, metabolic carbon balance and zonation of sublittoral macroalgae from King George Island (Antarctica). Mar Ecol Prog Ser 148:281–229

Gómez I, Wulff A, Roleda M et al (2009) Light and temperature demands of marine benthic microalgae and seaweeds in polar regions. Bot Mar 52:593–608

Gómez I, Navarro NP, Huovinen P (2019) Bio-optical and physiological patterns in Antarctic seaweeds: a functional trait based approach to characterize vertical zonation. Prog Oceanogr 174:17–27

Goutte A, Chevreuil M, Alliot F et al (2013) Persistent organic pollutants in benthic and pelagic organisms off Adélie land, Antarctica. Mar Pollut Bull 77:82–89

Grzymski J, Johnsen G, Sakshaug E (1997) The significance of intracellular self-shading on the bio-optical properties of brown, red and green macroalgae. J Phycol 33:408–414

Huovinen P, Gómez I (2012) Cold-temperate seaweed communities of the Southern Hemisphere. In: Wiencke C, Bischof K (eds) Seaweed biology: Novel insights into ecophysiology, ecology and utilization. Ecological studies, vol 219. Springer, Berlin, pp 293–313

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, Gómez I (2015) UV sensitivity of vegetative and reproductive tissues of three Antarctic macroalgae is related to differential allocation of phenolic substances. Photochem Photobiol 91:1382–1388

Huovinen PS, Oikari AOJ, Soimasuo MR, Cherr GN (2000) Impact of UV radiation on the early development of the giant kelp (*Macrocystis pyrifera*) gametophytes. Photochem Photobiol 72:308–313

Huovinen P, Ramírez J, Gómez I (2016) Underwater optics in sub-Antarctic and Antarctic coastal ecosystems. PLoS One 11(5):e0154887

Hurd CL, Hepburn CD, Currie KI et al (2009) Testing the effects of ocean acidification on algal metabolism: considerations for experimental designs. J Phycol 45:1236–1251

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, Lehmann H, Kirst GO, Wiencke C (1992a) Changes in the ultrastructure of *Prasiola crispa* ssp. *antarctica* under salinity stress. Plant Biol 105:41–46

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

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

Karsten U (2012) Seaweed acclimation to salinity and desiccation stress. In: Wiencke C, Bischof K (eds) Seaweed biology: Novel insights into ecophysiology, ecology and utilization. Ecological studies, vol 219. Springer, Berlin, Heidelberg, pp 87–107

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, Sawall T, West J, Wiencke C (2000) Ultraviolet sunscreen compounds in epiphytic red algae from mangroves. Hydrobiologia 432:159–171

Karsten U, Wulff A, Roleda MY, Müller R, Steinhoff F, Fredersdorf J, Wiencke C (2009) Physiological responses of polar benthic micro- and macroalgae to ultraviolet radiation. Bot Mar 52:639–654

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

Kornmann P, Sahling PH (1977) Meeresalgen von Helgoland. Benthische Grün-, Braun-und Rotalgen. Helgolander Meeresun 29:1–289

Kylin H, Skottsberg C (1919) Zur Kenntnis der Subantarktischen und Antarktischen Meeresalgen, II. Rhodophyceen. In: Nordenskjöld O (ed) Wissenschaftliche Ergebnisse der schwedischen Südpolarexpedition 1901–1903, Band IV, Lieferung 15. Stockholm, Lithographisches Institut des Generalstabs, 88 pp

Lamb IM, Zimmerman MH (1977) Benthic marine algae of the Antarctic Peninsula. Antarct Res Ser 23:129–229

Lignell A, Roomans GM, Pedersen M (1982) Localization of absorbed cadmium in *Fucus vesiculosus* by X-ray microanalysis. J Plant Physiol 105:103–109

Lorenz M, Schubert H, Forster RM (1997) *In vitro*- and *in vivo*-effects of ultraviolet-B radiation on the energy transfer in phycobilisomes. Photosynthetica 33:517–527

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

Lüning K, tom Dieck I (1989) Environmental triggers in algal seasonality. Bot Mar 32:389–397

Maier I (1993) Gamete orientation and induction of gametogenesis by pheromones in algae and plants. Plant Cell Environ 16:891–907

Marcías ML, Deregibus D, Saravia LA et al (2017) Life between tides: spatial and temporal variations of an intertidal macroalgal community at Potter Peninsula, South Shetland Islands, Antarctica. Estuar Coast Shelf Sci 187:193–203

Müller DG, Westermeier R, Peters A, Boland W (1990) Sexual reproduction of the Antarctic brown alga *Ascoseira mirabilis* (Ascoseirales, Phaeophyceae). Bot Mar 33:251–255

Navarro NP, Huovinen P, Gómez I (2016) Stress tolerance of Antarctic macroalgae in the early life stage. Rev Chil Hist Nat 89:5

Navarro NP, Huovinen P, Gómez I (2019) Photosynthetic characteristics of geographically disjunct seaweeds: a case study on the early life stages of Antarctic and Subantarctic species. Prog Oceanogr 174:28–36

Otto SP, Gerstein AC (2008) The evolution of haploidy and diploidy. Curr Biol 18:R1121–R1124

Quartino ML, Deregibus D, Campana GL 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(3):e58223

Raper JR, Flexer AS (1970) The road to diploidy with emphasis on a detour. Symposium of the Society of General Microbiology 20:401–432

Rautenberger R, Bischof K (2006) Impact of temperature on UV-susceptibility of two *Ulva* (Chlorophyta) species from Antarctic and Subantarctic regions. Polar Biol 28:988–996

Renger G, Voss M, Graber P, Schulze A (1986) Effect of UV irradiation on differential partial reactions of the primary processes of photosynthesis. In: Worrest RC, Caldwell MM (eds) Stratospheric ozone reduction, solar ultraviolet radiation and plant life. NATO ASI series, vol G8. Springer, Heidelberg, pp 171–184

Richter M, Rühle W, Wild A (1990) Studies on the mechanism of photosystem II photoinhibition I. a two-step degradation of D1-protein. Photosynth Res 24:229–235

Roleda M, Zacher K, Wulff A et al (2007) Photosynthetic performance, DNA damage and repair in gametes of the endemic Antarctic brown alga *Ascoseira mirabilis* exposed to ultraviolet radiation. Austral Ecol 32:917–926

Roleda MY, Zacher K, Wulff A et al (2008) Susceptibility of spores of different ploidy levels from Antarctic *Gigartina skottsbergii* (Gigartinales, Rhodophyta) to ultraviolet radiation. Phycologia 47:361–370

Roleda MY, Campana G, Wiencke C et al (2009) Sensitivity of Antarctic *Urospora penicilliformis* (Ulotrichales, Chlorophyta) to ultraviolet radiation is life stage dependent. J Phycol 45:600–609

Roleda MY, Morris JN, McGraw CM, Hurd CL (2011) Ocean acidification and seaweed reproduction: increased CO_2 ameliorates the negative effect of lowered pH on meiospore germination in the giant kelp *Macrocystis pyrifera* (Laminariales, Phaeophyceae). Glob Chang Biol 18:854–864

Salles S, Aguilera J, Figueroa FL (1996) Light field in algal canopies: changes in spectral light ratios and growth of *Porphyra leucosticta*. Thur. In Le Jol. Sci Mar 60:29–38

Skottsberg C (1953) On two collections of Antarctic marine algae. Arkiv Botanik Serie 2 2:531–566

Swanson AK, Druehl LD (2000) Differential meiospore size and tolerance of ultraviolet light stress within and among kelp species along a depth gradient. Mar Biol 136:657–664

Tom Dieck I (1989) Vergleichende Untersuchungen zur Ökophysiologie und Kreuzbarkeit innerhalb der digitaten Sektion der Gattung *Laminaria*. PhD thesis, University of Hamburg, Hamburg, Germany, 168 pp

Vass I (1997) Adverse effects of UV-B light on the structure and function of the photosynthetic apparatus. In: Pessarakli M (ed) Handbook of photosynthesis. Marcel Dekker Inc., New York, pp 931–949

Weykam G, Wiencke C (1996) Seasonal photosynthetic performance of the endemic Antarctic alga *Palmaria decipiens* (Reinsch) Ricker. Polar Biol 16:357–361

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 (1990) Sexual reproduction, life history, and early development in culture of the Antarctic brown alga *Himantothallus grandifolius* (Desmarestiales, Phaeophyceae). Phycologia 29:9–18

Wiencke C, Clayton MN (2002) In: Wägele JW, Sieg J (eds) Antarctic seaweeds. Synopses of the Antarctic benthos, vol 9. Gantner, Ruggell, Lichtenstein. 239 pp

Wiencke C, Stolpe U, Lehmann H (1991) Morphogenesis of the brown alga *Desmarestia antarctica* cultivated under seasonally fluctuating Antarctic daylengths. Ser Cient INACH 41:65–78

Wiencke C, Clayton MN, Schulz D (1995) Life history, reproductive morphology and development of the Antarctic brown alga *Desmarestia menziesii* J. Agardh. Plant Biol 108:201–208

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, Gómez I, Pakker H, Flores-Moya A, Altamirano M, Hanelt D, Bischof K, Figueroa F-L (2000) Impact of UV radiation on viability, photosynthetic characteristics and DNA of brown algal zoospores: implications for depth zonation. Mar Ecol Prog Ser 197:217–229

Wiencke C, Roleda MY, Gruber A et al (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 et al (2007) Life strategy, ecophysiology and ecology of seaweeds in polar waters. Rev Environ Sci Biotechnol 6:95–126

Wiencke C, Gómez I, Dunton K (2009) Phenology and seasonal physiological performance of polar seaweeds. Bot Mar 52:585–559

Wünschmann G, Brand JJ (1992) Rapid turnover of a component required for photosynthesis explains temperature dependence and kinetics of photoinhibition in a cyanobacterium, *Synechococcus* 6301. Planta 186:426–433

Wynne MJ (1982) Observations on four species of Delesseriaceae (Rhodophyta) from the South Sandwich Islands, the Antarctic. Contr Univ Mich Herb 15:325–337

Zacher K (2014) The susceptibility of spores and propagules of Antarctic seaweeds to UV and photosynthetically active radiation — field versus laboratory experiments. J Exp Mar Biol Ecol 458:57–63

Zacher K, Roleda MY, Hanelt D, Wiencke C (2007) UV effects on photosynthesis and DNA in propagules of three Antarctic seaweeds (*Adenocystis utricularis*, *Monostroma hariotii* and *Porphyra endiviifolium*). Planta 225:1505–1516

Zacher K, Roleda MY, Wulff A et al (2009) Responses of Antarctic *Iridaea cordata* (Rhodophyta) tetraspores exposed to ultraviolet radiation. Phycol Res 57:186–193