Antarctic Science 15 (4): 449–457(2003) © Antarctic Science Ltd Printed in the UK DOI: 10.1017/S0954102003001550

Experimental investigation of seasonal development in six Antarctic red macroalgae

ANGELIKA L. DUMMERMUTH and CHRISTIAN WIENCKE

Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, D-27570 Bremerhaven, Federal Republic of Germany
adummermuth@awi-bremerhaven.de

Abstract: The phenology of six Antarctic red macroalgae, *Delesseria salicifolia* Reinsch, *Gymnogongrus antarcticus* Skottsberg, *Gymnogongrus turquetii* Hariot, *Hymenocladiopsis crustigena* Moe, *Kallymenia antarctica* Hariot and *Phyllophora ahnfeltioides* Skottsberg, was investigated in a two-year culture study under fluctuating daylengths imitating the conditions of King George Island, South Shetland Islands. The algae were cultured at 0°C in filtered, nutrient enriched seawater under photon fluence rates of 3, 10, 25, 50 µmol photons m^{-2} s^{-1}. All species are classified as season anticipators, starting growth in late winter–spring and stopping growth before the summer solstice. Formation of new blades was observed from January/February onwards in most of the species. Carpospore formation was observed in *K. antarctica* in early summer. Growth was light saturated at photon fluence rates of 3 µmol photons m^{-2} s^{-1} in *D. salicifolia* and at 10 µmol photons m^{-2} s^{-1} in the other species, corresponding to an annual light dose of 31.4 and 157 mol photons m^{-2}. The results show that this type of life strategy is typical for species from the Antarctic and give further evidence on the high degree of shade adaptation of Antarctic algae and predict a lower distribution limit for these species at 37 ± 15 m and 23 ± 10 m, respectively.

Received 7 February 2003, accepted 3 June 2003

Key words: growth, life strategies, morphological development, phenology, Rhodophyta, seaweeds

Introduction

Studies on Antarctic macroalgae have previously been focused mostly on the description of individual species, their life histories and on basic ecophysiological data (Wiencke 1996). Much information has been obtained on their temperature (Wiencke & tom Dieck 1989, 1990, Bischoff-Bäsmann & Wiencke 1996) and light requirements (Wiencke & Fischer 1990, Wiencke *et al.* 1993, Weykam *et al.* 1996, Gomez *et al.* 1997) in the context of geographical distribution and depth zonation. Relatively detailed information is available on the phenology of seven brown algal species, in particular on *Ascoseira mirabilis* and *Desmarestia menziesii* (Gomez *et al.* 1995a, 1995b, 1997, Gomez & Wiencke 1998, Wiencke 1990a). In contrast, the phenology of the algal group with the highest species number in the Antarctic region (Clayton 1994), the red algae, is known for only three species, with most detail for *Palmaria decipiens* (Wiencke 1990b, Weykam & Wiencke 1996, Weykam *et al.* 1997, Lüder 2001, Lüder *et al.* 2002). Six of the brown algal species studied grow and reproduce in late winter/spring and are classified as season anticipators according to Kain (1989). Only one, *Adenocystis utricularis*, responded in an opportunistic way in summer (Wiencke 1990a). From the three red algal species one, *Palmaria decipiens*, is a season anticipator and the two others *Iridaea cordata* and *Gigartina skottsbergii*, are season responders (Wiencke 1990b).

In order to improve our knowledge about the seasonal development of red algae from the Antarctic region we cultivated six red algal species for two years under seasonally fluctuating daylengths, imitating Antarctic conditions. In the Antarctic region, the light regime is the most important parameter determining the phenology of macroalgae. Temperature and nutrient levels - other factors influencing the seasonal development of seaweeds (Lüning 1980a, 1980b, Mann 1982, Lüning & tom Dieck 1989) - are almost constant throughout the year (Gordon & Molinelli 1982, Clarke *et al.* 1988, Drew & Hastings 1992). Our method, using seasonally fluctuating Antarctic daylengths, was designed to monitor seasonal development of specific Antarctic species as shown in various studies (Wiencke 1990a, 1990b, Gomez & Wiencke 1996, 1998, Weykam & Wiencke 1996). In order to obtain additional information on the variation of phenology and anatomy in different water depths, the species were cultivated at various photon fluence rates. The method has also been successfully used in studies from other regions (Lüning 1991, Lüning & tom Dieck 1989).

The main aim of this study was to determine the seasonal development of ecologically important red algae and to classify the species by their life strategy. The majority of the Antarctic species studied so far are season anticipators whose phenology is finely tuned to the strong seasonal changes seen in the light conditions in the Antarctic. Our results will show that this type of life strategy is typical for seaweeds from the Antarctic, especially for the species tested here, which are all endemics (*Delesseria salicifolia*, *Gymnogongrus antarcticus*, *Hymenocladiopsis crustigena*,

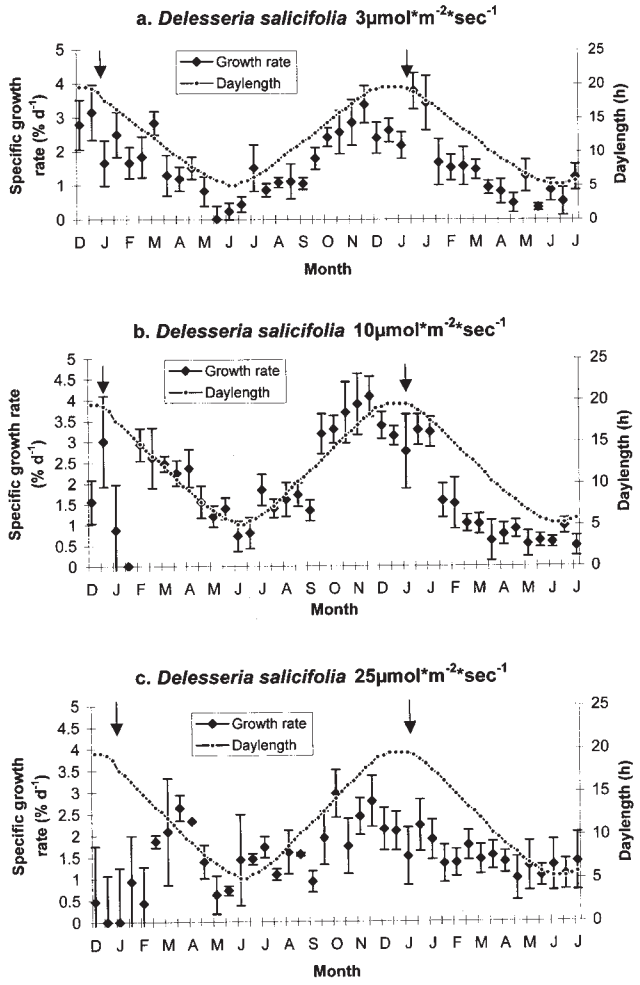

Fig. 1. Specific growth rates of *Delesseria salicifolia* grown under photon fluence rates of **a.** 3, **b.** 10, and **c.** 25 µmol m^{-2} s^{-1} and daylengths adjusted to the seasonal variation on King George Island (Wiencke 1990a). Arrows indicate the formation of blade initials. Double appearance of months is due to a month with four samplings.

Phyllophora ahnfeltioides), or have their centre of distribution in the Antarctic region (*Gymnogongrus turquetii*, *Kallymenia antarctica*) according to Wiencke & Clayton (2002). Moreover, we will demonstrate the high degree of shade adaptation and predict their lower distribution limit by use of recent data on the underwater light conditions.

Materials and methods

The following species and life history stages were investigated: *Delesseria salicifolia* Reinsch (female gametophytes), *Gymnogongrus antarcticus* Skottsberg (female gametophytes), *Gymnogongrus turquetii* Hariot (=*Phyllophora appendiculata* Skottsberg; vegetative), *Hymenocladiopsis crustigena* Moe (tetrasporophyte), *Kallymenia antarctica* Hariot (female gametophytes) and

Table I. Minimum, maximum and average growth rates of the investigated species and p-values of a pair wise students *t*-test. Values obtained during the acclimation period of six months excluded.

Species/photon fluence rate	Min (% d^{-1})	Max (% d^{-1})	Average (% d^{-1})	*t*-test (pairwise) *P*-values
Delesseria salicifolia				
3 µmol m^{-2} sec^{-1}	0.23	3.78	1.58	3/10 ($P < 0.0244$)*
10 µmol m^{-2} sec^{-1}	0.49	4.08	1.82	3/25 ($P < 0.5640$),
25 µmol m^{-2} sec^{-1}	0.43	2.96	1.57	10/25 ($P < 0.0234$)*
Gymnogongrus antarcticus				
3 µmol m^{-2} sec^{-1}	0.33	2.35	0.90	
10 µmol m^{-2} sec^{-1}	0.45	4.02	1.73	3/10 ($P < 0.0001$)***
25 µmol m^{-2} sec^{-1}	0.39	3.97	1.70	3/25 ($P < 0.0001$)***
50 µmol m^{-2} sec^{-1}	0.35	4.15	1.80	3/50 ($P < 0.0001$)***
Gymnogongrus turquetii				
3 µmol m^{-2} sec^{-1}	0.26	1.91	0.94	3/10 ($P < 0.0001$)***
10 µmol m^{-2} sec^{-1}	0.21	2.76	1.23	3/25 ($P < 0.1397$),
25 µmol m^{-2} sec^{-1}	0.25	2.99	1.06	10/25 ($P < 0.0054$)**
Hymenocladiopsis crustigena				
3 µmol m^{-2} sec^{-1}	0.23	1.79	0.80	3/10 ($P < 0.0001$)***,
10 µmol m^{-2} sec^{-1}	0.23	3.51	1.26	3/25 ($P < 0.0001$)***
25 µmol m^{-2} sec^{-1}	0.35	4.10	1.57	10/25 ($P < 0.01$)**
Kallymenia antarctica				
3 µmol m^{-2} sec^{-1}	0.13	1.31	0.64	3/10 ($P < 0.0001$)***
10 µmol m^{-2} sec^{-1}	0.35	2.78	1.23	3/25 ($P < 0.0001$)***,
25 µmol m^{-2} sec^{-1}	0.50	1.17	1.17	10/25 ($P < 0.0066$)**
Phyllophora ahnfeltioides				
3 µmol m^{-2} sec^{-1}	0.13	1.03	0.47	
10 µmol m^{-2} sec^{-1}	0.22	1.69	0.79	3/10 ($P < 0.0001$)***
25 µmol m^{-2} sec^{-1}	0.29	1.87	0.84	3/25 ($P < 0.0001$)***

Phyllophora ahnfeltioides Skottsberg (vegetative). The algae were isolated as spores or as small thallus parts from Potter Cove, tributary inlet of Maxwell Bay, King George Island, South Shetland Islands and subsequently maintained as unialgal cultures in the culture collection of the Alfred Wegener Institute in dim light and seasonally fluctuating Antarctic daylengths (see below). From most species herbarium specimen were prepared and stored in the collection of the Alfred Wegener Institute in Bremerhaven.

For the experiments the algae were cultivated in temperature controlled rooms at a temperature of 0 ± 1°C and illuminated with cool-white fluorescent tubes (Osram L58/W12). Light intensities of 3, 10, 25 and 50 µmol m^{-2} sec^{-1} were adjusted by use of a Licor Li-185B quantameter (Lincoln, USA) equipped with a Li-190 B quantum sensor. Daylength was adjusted weekly according to the seasonal variation of daylength at King George Island, 62°12'S, 58°58'W (Wiencke 1990a). The plants were cultivated in membrane-filtered seawater (Sartorius Sartoban II, pore size 0.2 µm) from the North Sea enriched with nutrients after Provasoli (Stein 1973). The medium was changed every two weeks to maintain nitrogen and phosphate levels above 0.6 and 0.025 moles m^{-3}, respectively. The culture experiment was started using thallus pieces of < 2 cm with a minimum fresh weight of 50 mg just before the summer

https://doi.org/10.1017/S095410200300155X Published online by Cambridge University Press

solstice (daylength 20 hours).

Growth rates were determined by recording fresh weight of algae after blotting with paper tissue using the following equation:

$$\text{specific growth rate } \left(\%\text{day}^{-1}\right) = \frac{100\,1n\ W_t\ W_0^{-1}}{t}$$

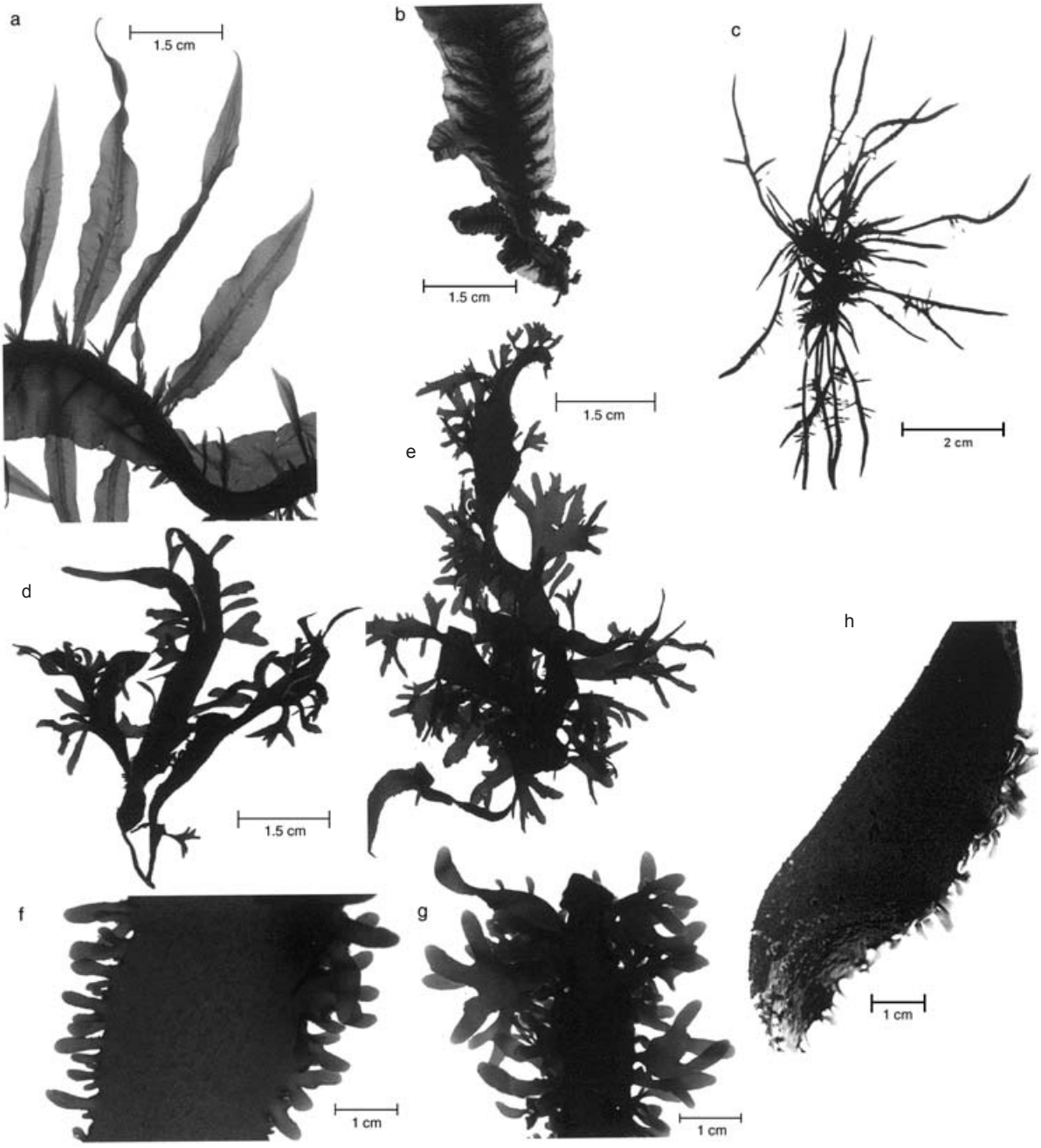

Fig. 2. Variation of thallus morphology in the studied species (photographs taken in May, second year of the experiment). **a.** *Delesseria salicifolia*, habit of a two-year old individual grown under a photon fluence rate of 3 µmol m^{-2} s^{-1} showing first and second year blades and new blade initials. **b.** *Delesseria salicifolia* cultured under a photon fluence rate of 10 µmol m^{-2} s^{-1}, blade lamina polystromatic. **c.** *Phyllophora ahnfeltioides*, habit of a plant grown under a photon fluence rate of 3 µmol m^{-2} s^{-1}. **d.** *Gymnogongrus antarcticus*, habit grown under a photon fluence rate of 3µmol m^{-2} s^{-1}. **e.** *Gymnogongrus antarcticus*, habit grown under a photon fluence rate of 10µmol m^{-2} s^{-1}. **f.** *Gymnogongrus turquetii*, detail of thallus grown under a photon fluence rate of 3 µmol m^{-2} s^{-1} showing lanceolate blade initials at the margin. **g.** *Gymnogongrus turquetii*, detail of thallus grown under a photon fluence rate of 10 µmol m^{-2} s^{-1} showing dense packing of several weeks old subdichotomously branched blades. **h.** *Hymenocladiopsis crustigena*, habit of a plant grown under a photon fluence rate of 3 µmol m^{-2} s^{-1}. Formation of new blades at the margin and surface of the thallus.

https://doi.org/10.1017/S095410200300155X Published online by Cambridge University Press

where W_0 = initial fresh weight, W_t = fresh weight on day t, and t = time interval (Wiencke & tom Dieck 1989). Five individuals per photon fluence rate were used for the growth measurements and mean values with standard deviation calculated. For the calculation of minimum, maximum, average growth rates of the first six months were not taken into account as the data are more scattered during the acclimation process to the fluctuating daylength regime. Statistical significance of average growth rates was calculated by a pairwise student's *t*-test using the program Statistica (Statsoft Inc, Tulsa, USA).

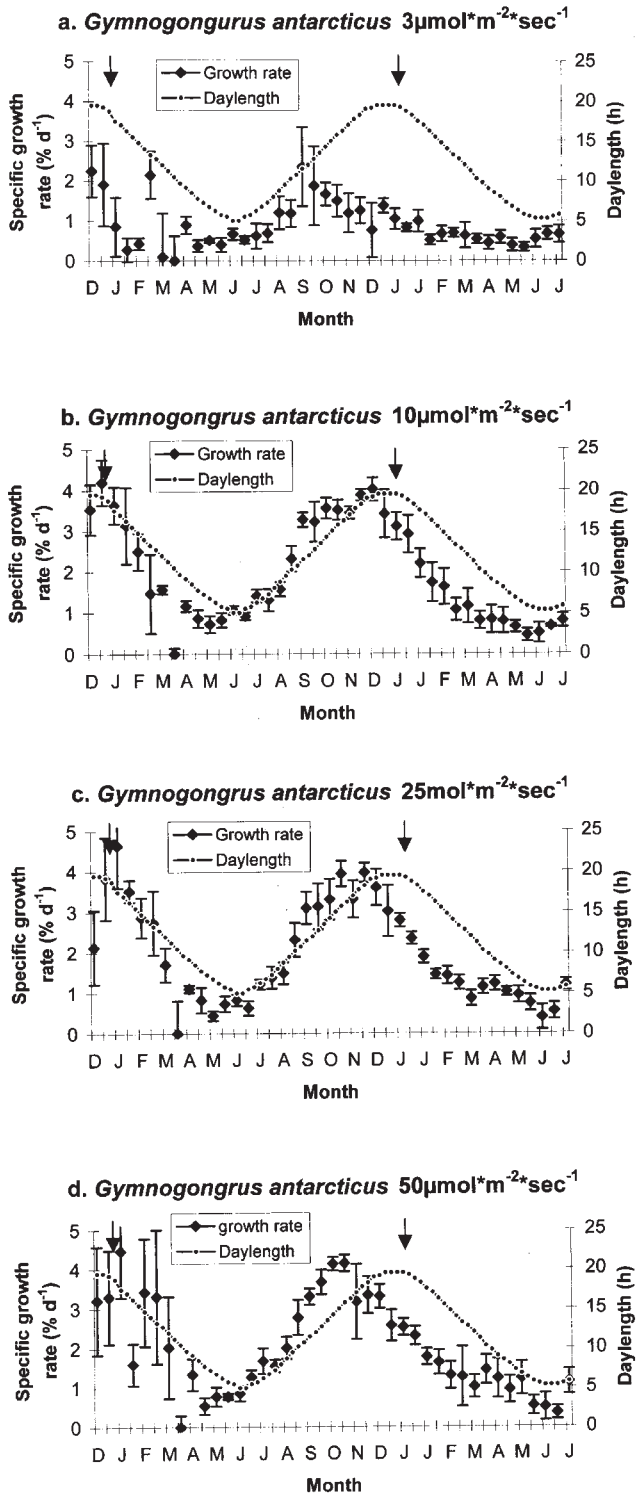

Fig. 3. Specific growth rates of *Gymnogongrus antarcticus* grown under photon fluence rates of **a.** 3, **b.** 10, **c.** 25, and **d.** 50 µmol m^{-2} s^{-1}. Arrows indicate formation of blade initials.

Results

During the first half year after the start of the experiment, growth rates of *Delesseria salicifolia* varied considerably but principally declined (Fig. 1a–c). In August, growth rates started to increase and maximum growth rates were generally measured in October to November. In December growth rates started to decline under all conditions. Highest average growth rates were measured in thalli exposed to 10 µmol m^{-2} s^{-1}, differing significantly from average growth rates at 3 µmol m^{-2} s^{-1} ($P < 0.0244$) and 25 µmol m^{-2} s^{-1} ($P < 0.0234$, Table I).

At low photon fluence rates (3–10 µmol m^{-2} s^{-1}) *D. salicifolia* exhibited the characteristic thallus morphology with monostromatic leaf-like blades and oppositely branched midribs (Fig. 2a). When exposed to 25 µmol m^{-2} s^{-1} the structure of the whole blade became polystromatic (Fig. 2b). Degeneration of the monostromatic parts of the lamina of the largest blades started in January in individuals exposed to 10 and 25 µmol m^{-2} s^{-1}. The bleaching process went on until the whole blade was colourless except the midrib. In January to March 2 mm long blade initials grew out from the midribs under all conditions (Fig. 2a).

Gymnogongrus antarcticus showed an irregular growth pattern in the first six months of the study (Fig. 3a–d). In June, growth rates were low under all light conditions. With increasing daylength in July, specific growth rates rose under all four experimental set-ups until maximum growth rates were reached in August to November. Subsequently, growth rates decreased continuously until the winter solstice in July under all conditions. Similarly high growth rates were measured in thalli exposed to 10, 25 and 50 µmol m^{-2} s^{-1}, whereas significantly lower growth rates were obtained at 3 µmol m^{-2} s^{-1} ($P < 0.0001$; Table I).

Formation of new blades started in January at the margins of the thallus. Within the following three months, 1 cm large blades were formed, which grew out in the next growth period. At 3 µmol m^{-2} s^{-1} the thalli were small, thin and light red, at 10 µmol m^{-2} s^{-1} the thallus was larger, cartilaginous and more darkly pigmented. Fronds at 25 and 50 µmol m^{-2} s^{-1} were very cartilaginous, brownish red and formed dense tufts (Fig. 2d & e).

Growth rates of *Gymnogongrus turquetii* exhibited a considerable variation at first, but were low at the end of the acclimation process in June under all conditions. They started to rise in July reaching maximum values in August

https://doi.org/10.1017/S095410200300155X Published online by Cambridge University Press

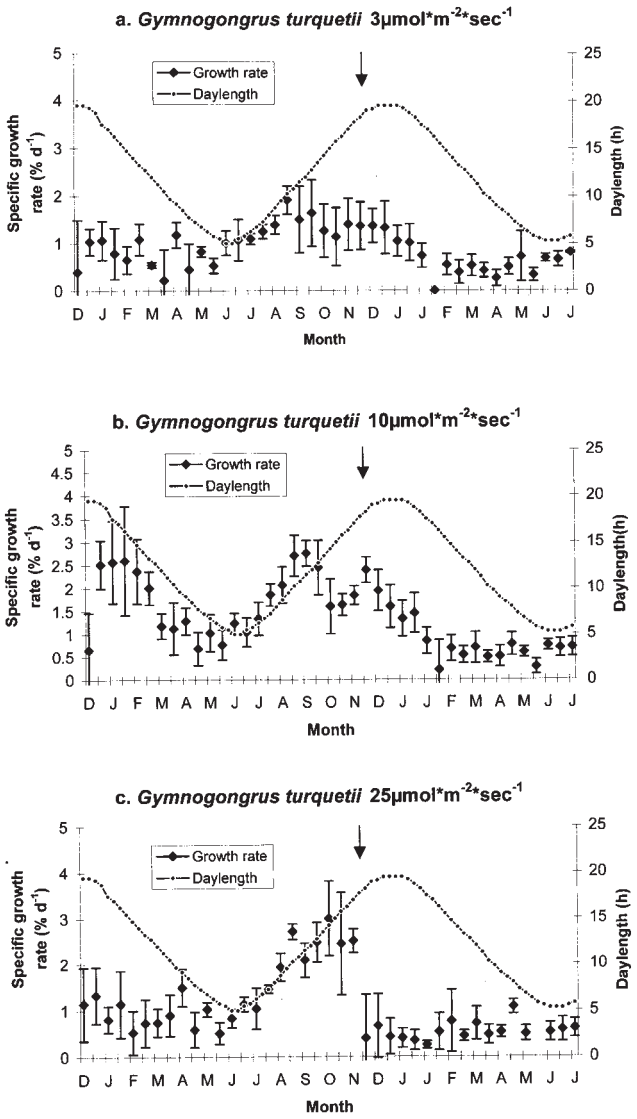

Fig. 4. Specific growth rates of *Gymnogongrus turquetii* grown under photon fluence rates of **a.** 3, **b.** 10, and **c.** 25 µmol m^{-2} s^{-1}. Arrows indicate formation of blade initials.

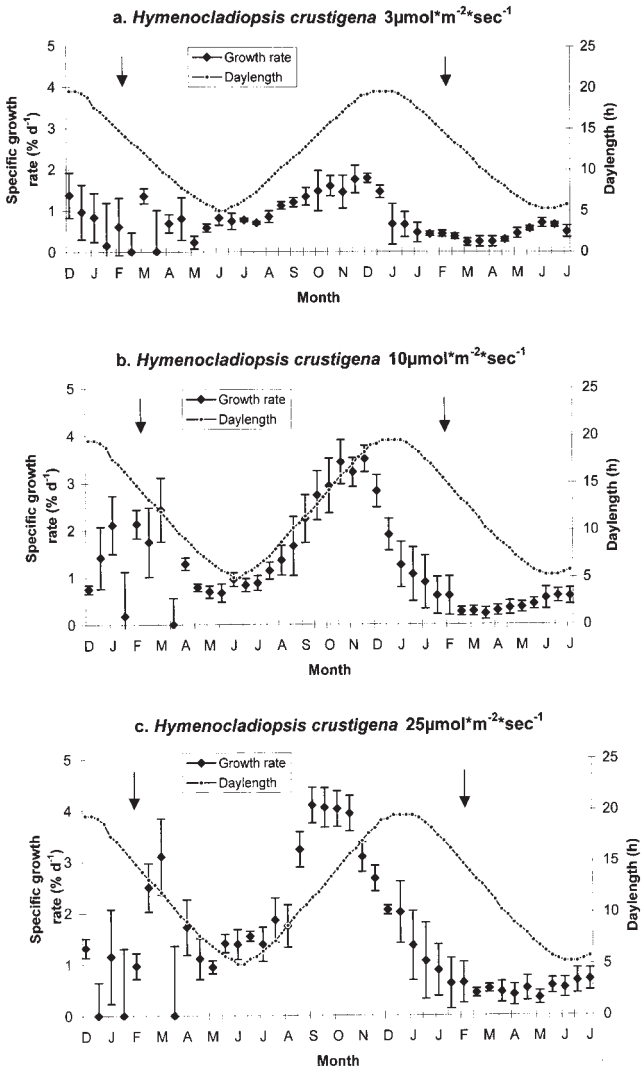

Fig. 5. Specific growth rates of *Hymenocladiopsis crustigena* grown under photon fluence rates of **a.** 3, **b.** 10, and **c.** 25 µmol m^{-2} s^{-1}. Arrows indicate formation of blade initials.

to October under all conditions (Fig. 4a–c). Later, growth rates declined until January/February and remained low with minimum values of 0.21–0.26 % d^{-1} until the winter solstice. A strong dormancy was observed during this period in thalli exposed to 25 µmol m^{-2} s^{-1} (Fig. 4c). Thalli exposed to 10 µmol m^{-2} s^{-1} and 25 µmol m^{-2} s^{-1} showed similar high growth rates, whereas growth rates at 3 µmol m^{-2} s^{-1} were lower (Table I). In contrast, average growth rates were similar when exposed to 3 and 25 µmol m^{-2} s^{-1} differing significantly to average growth rates of thalli grown at 10 µmol m^{-2} s^{-1} ($P < 0.0001$, $P < 0.0054$, Table I).

New blades started to grow out from the blade margins in November to December. By May, the outgrowths reached a size of 1–1.5 cm (Fig. 2f & g). Overall, the healthiest plants grew at 3 µmol m^{-2} s^{-1} whereas plants exposed to 10 and 25 µmol m^{-2} s^{-1} were partially bleached under summer conditions.

In *Hymenocladiopsis crustigena* growth rates varied at first considerably in the first 6 months of the experiment and decreased to low values at the winter solstice. From July onwards growth rates increased (Fig. 5a–c) and thalli exposed to 25 µmol m^{-2} s^{-1} exhibited a growth maximum in September, decreasing then from October onwards until February. Under 3 and 10 µmol m^{-2} s^{-1} highest growth rates were attained in September–November. From December onwards they decreased, reaching the annual minimum between January and June. Lowest growth rates were recorded at 3 µmol m^{-2} s^{-1} whereas average growth rates were almost twice as high in individuals cultivated at 10 and 25 µmol m^{-2} s^{-1} differing significantly to average growth rate attained at 3 µmol m^{-2} s^{-1} ($P < 0.0001$, Table I). In February, lanceolate blade initials were formed at the margins and the surface of the main blade in a shape which

https://doi.org/10.1017/S095410200300155X Published online by Cambridge University Press

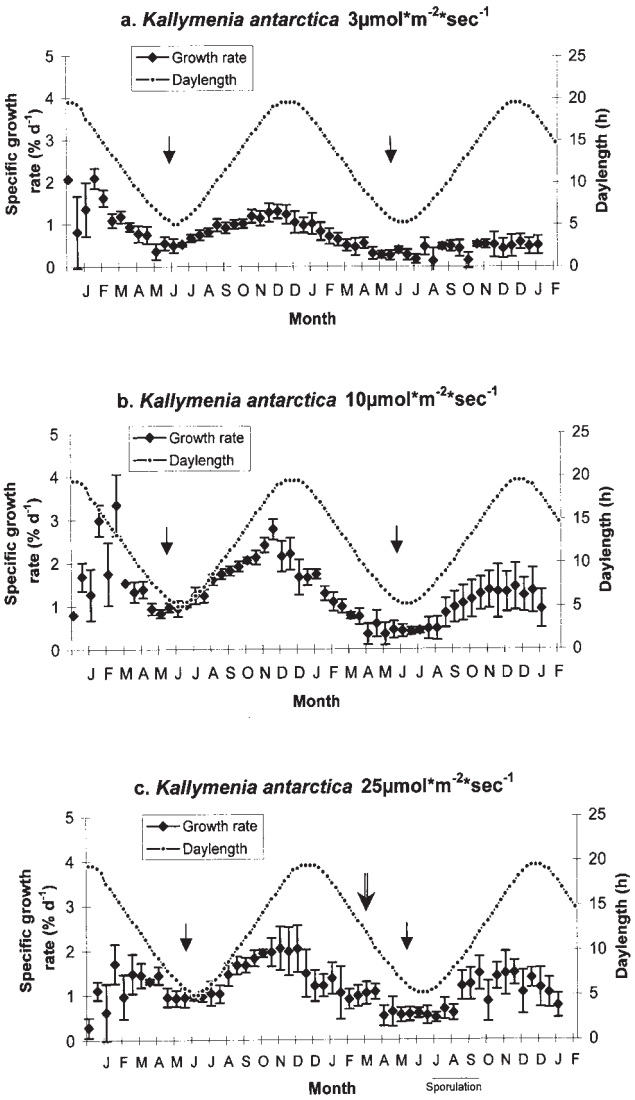

Fig. 6. Specific growth rates of *Kallymenia antarctica* grown under photon fluence rates of **a.** 3, **b.** 10, and **c.** 25 µmol m^{-2} s^{-1}. Arrows indicate formation of blade initials; the double arrow indicates the formation of cystocarps.

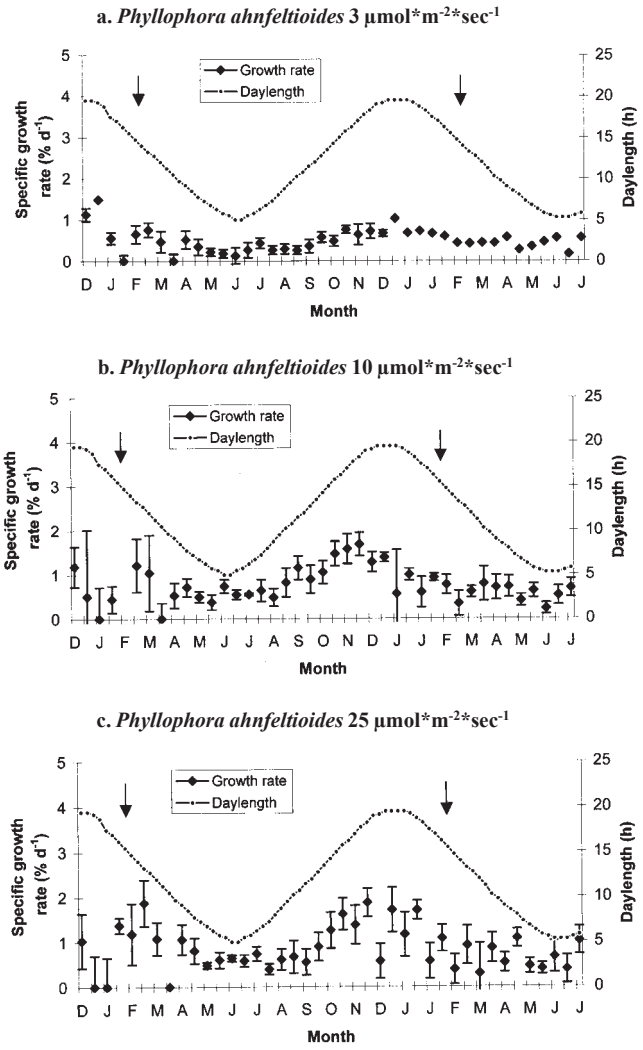

Fig. 7. Specific growth rates of *Phyllophora ahnfeltioides* grown under photon fluence rates of **a.** 3, **b.** 10, and **c.** 25 µmol m^{-2} s^{-1}. Arrows indicate formation of blade initials.

divided subdichotomously after 10 weeks of growth to a size 5–10 mm (Fig. 2h).

Kallymenia antarctica exhibited an irregular growth pattern during the acclimation period and showed low growth rates around the time of the winter solstice (Fig. 6a–c). In July, growth rates started to rise in all experimental conditions until maxima were reached in August to October. Individuals cultivated at 3 µmol m^{-2} s^{-1} showed significantly lower growth rates throughout the year compared to individuals kept at 10 and 25 µmol m^{-2} s^{-1} ($P < 0.0001$, Table I). New blades were formed on the holdfast in this species from the end of May onwards, reaching a size of up to 7 mm within six weeks. In apices of thalli exposed to 25 µmol m^{-2} s^{-1} the medullary cells were often considerably expanded. Cystocarps developed from March onwards and sporulation occurred from July to September in individuals exposed to 25 µmol m^{-2} s^{-1}.

At the end of the acclimation period in June growth rates of *Phyllophora ahnfeltioides* were low. From July onwards growth rates increased until October/November and then continuously declined until June to minimum values (Fig. 7a–c). The species exhibited the lowest growth rates of all the six investigated species. At 3 µmol m^{-2} s^{-1} average growth rate was significantly lower than in thalli exposed to 10 and 25 µmol m^{-2} s^{-1} ($P < 0.0001$, Table I). Formation of new fronds was initiated in summer, starting in February, arising from all thallus parts. The lanceolate outgrowths attained a length of about 4 mm within three months (Fig. 2c). At 25 µmol m^{-2} s^{-1} dense tufts were formed, exhibiting loss of pigments in the inner part of the tufts.

https://doi.org/10.1017/S095410200300155X Published online by Cambridge University Press

Discussion

The results obtained in this study considerably extend our knowledge about the phenology of Antarctic seaweeds. The seasonal growth pattern of Antarctic macroalgae has so far been demonstrated only in 11 species (Gain 1912, Wiencke 1990a, 1990b, Drew & Hastings 1992, Gomez & Wiencke 1996). Six of these species are season anticipators after the classification of Kain (1989), starting their growth in late winter/spring. They are all endemic to Antarctica and live in the lower eulittoral to sublittoral. The season responders, in contrast, start growth in spring to summer, occur in the eulittoral and upper sublittoral and are widely distributed in Antarctic, sub-Antarctic to cold-temperate waters. As our data show, all of the species investigated here belong to the season anticipators group.

Season responders grow predominantly when primary factors (temperature, light, nutrients etc.) are favourable for the species (Kain 1989, Lüning & tom Dieck 1989). The seasonal development of season anticipators is, in contrast, governed either by circannual rhythms or photoperiodisms (Kain 1989, Lüning & tom Dieck 1989, tom Dieck 1991, Lüning 1991, 1993). Daylength appears to be the principal driver, as temperature and nutrients are quite stable throughout the whole year in Antarctic shallow waters (Clarke *et al.* 1988, Drew & Hastings 1992).

The period of highest growth rates in the species studied here is generally between September and November. In *Hymenocladiopsis crustigena*, however, the seasonal growth peak is shifted anticlockwise to August under high light conditions (25 µmol m^{-2} s^{-1}; Fig 5). Similar results have been obtained already in other season anticipators from the Antarctic, e.g. in the brown algae *Himantothallus grandifolius* and *Phaeurus antarcticus* (Wiencke 1990a). This shows that photon fluence rate can modify the phenology of season anticipators, which is principally controlled by daylength. In the field the seasonal growth peak of the species should therefore be later in the season at deeper water depths and earlier in more shallow waters.

The increase of growth rates in late winter/spring in season anticipators is based on the development of new blades. One important new result obtained in this study is that the blade initials are already formed in the autumn, during a period of general decline of growth rates in all species except *Kallymenia antarctica*. In the latter species, blade initials are formed in the winter as they are in *Palmaria decipiens* (Wiencke 1990b, Weykam *et al.* 1997). Similarly, the blade initials of the northern Hemisphere *Delesseria sanguinea* are formed in response to short days occurring after mid winter (Kornmann & Sahling 1977, Kain 1982, 1987). The transformation of primary laterals into side branches in the Antarctic brown alga *Desmarestia anceps*, another season anticipator, starts in August (Wiencke *et al.* 1996).

The decrease of growth rates in *Delesseria salicifolia* in January/February is the result of degeneration of the monostromatic parts of the blade lamina. It starts as a bleaching of the thallus (Fig. 2b) and begins at the margins. Degeneration proceeds until only the midribs remain, similarly as described for (sub-)Antarctic *D. lancifolia* (Ricker 1987) and the Northern Hemisphere *D. sanguinea* (Kornmann & Sahling 1977). In the latter species it was demonstrated that radioactively labelled assimilates are transported back to the midrib and used for the later formation of new blades (Schmitz, University of Cologne, personal communication 2000). This might also occur in the species studied here.

Kallymenia antarctica was the only species in this study completing its life cycle with carpospore-formation between June and August. The first cystocarps were found in March. This is supported by results from Lamb & Zimmermann (1977), who found (presumably immature) cystocarps in thalli of *K. antarctica* in January. In *D. salicifolia*, cystocarps and tetrasporangia were found by Wynne (1982) in late winter samples. Similarly, spermatangia, cystocarps and tetrasporangia in *D. sanguinea* are always formed in the winter season (Kornmann & Sahling 1977). In *Gymnogongrus antarcticus* cystocarps are usually formed in the summer as recorded by Cormaci *et al.* (1992) and Skottsberg (1953). Cystocarpic plants of *G. turquetii* were collected by Kylin & Skottsberg (1919) and Skottsberg (1953) in May, June and August. In *Phyllophora ahnfeltioides* cystocarps were found between May and June (Kylin & Skottsberg 1919). No data are available on seasonal reproduction in *Hymenocladiopsis crustigena*.

In a recent survey of Antarctic macroalgae (Wiencke & Clayton 2002) the species investigated were all classified as shade-adapted species based on the available photosynthetic performance data. Such species are characterised by an efficient light absorption at low photon fluence rates as indicated by high α values (i.e. slope in the light-limited portion of the photosynthesis–light curve) and low light compensation and saturation points (Wiencke *et al.* 1993, Weykam *et al.* 1996, Eggert & Wiencke 2000). Foliose species show highest α values in comparison to leathery or terete algae. This is reflected by the different light requirements for growth determined here. *Delesseria salicifolia* is the only species with a membranous-foliose morphology and shows almost the same growth rates at all photon fluence rates tested. (Table I). All other species are morphologically thick and exhibit considerably lower growth rates at 3 µmol m^{-2} s^{-1} compared to the higher photon fluence rates. This means that 10 µmol m^{-2} s^{-1} represents the lowest irradiance under which sufficient growth of these terete and leathery species is possible. In contrast, the foliose *D. salicifolia* is able to grow in more shady locations.

Thallus morphology is influenced by the applied irradiances. Thalli, especially of *Gymnogongrus*

https://doi.org/10.1017/S095410200300155X Published online by Cambridge University Press

antarcticus, *Kallymenia antarctica* are more compact, thicker and darker and have a higher surface-to-volume ratio under the higher photon fluence rates tested. In *G. turquetii*, blades were partially bleached during exposure to photon fluence rates ≥ 10 µmol m^{-2} s^{-2} indicating a susceptibility of the species to high photon fluence rates. In *Phyllophora ahnfeltioides* and *Gymnogongrus antarcticus* the density of branches and new blades was higher at photon fluence rates ≥ 25 µmol m^{-2} s^{-2}. In this way the degree of self shading is increased, and as a result the degree of high light stress is reduced. The photon fluence rates applied *per se* are certainly not regarded as high light conditions. But there are obviously cumulative effects under Antarctic summer conditions at daylengths up to 20 h, which may lead in fact to light stress. This interpretation is supported by the fact that growth rates of the latter two species under high photon fluence rates were often even somewhat lower compared to those obtained at 10 µmol m^{-2} s^{-2}.

The minimum light requirement for sufficient growth of *Delesseria salicifolia* is < 3 µmol m^{-2} s^{-1}, probably 2 µmol m^{-2} s^{-1}, corresponding to an annual light dose of 31.4 mol m^{-2}. The minimum light requirement of the other species is 10 µmol m^{-2} s^{-1}, corresponding to an annual light dose of 157.0 mol m^{-2}. Therefore, the minimum annual light requirements for growth are in a similar range as in other red algal species from the Antarctic examined so far (Wiencke 1990b). In particular, for *Palmaria decipiens* a minimum annual light dose of 47.1 mol m^{-2}, and for *Iridaea cordata* and *Gigartina skottsbergii* of 143.3 mol m^{-2} $year^{-1}$ has been determined (Wiencke 1990a). The light requirements of brown algae are in the same range (Wiencke 1990a).

Can these data be used to predict the lower depth distribution limit of the species studied? The water depth for 1% light is generally regarded as the lower distribution limit of canopy species especially of kelps (Lüning 1990, Sommer 1998). On Helgoland, the kelp *Laminaria hyperborea* receives an annual light dose of 71.2 mol m^{-2} at the 1% depth (Lüning & Dring 1979). The species tested here need a minimum annual light dose of 31.4 or 157.0 mol m^{-2} corresponding to water depths of 0.44 and 2.21%, respectively, using the above relation. According to the latest data on the biooptical characteristics in the Antarctic Peninsula–South Shetland Islands region (Figueroa 2002), these % surface radiation depths correspond to water depths of 37 ± 15 and 23 ± 10 m, respectively. These values are likely to be somewhat underestimated as the measurements were done in December and January, known as months with frequent phytoplankton blooms and high water turbidity (Drew & Hastings 1992, Klöser *et al.* 1993). The data confirm previous estimates of the lower depth distribution limit of other red as well as on other brown and green macroalgae from King George Island (Wiencke 1990a, 1990b). The use of unmanned submersible remotely operating vehicles equipped with video cameras and sampling devices could resolve this question.

Acknowledgements

We thank C. Langreder and C. Daniel for excellent technical assistance, I. Bartsch and M. Schoenwaelder for critically reading the manuscript. This project was financially supported by the German Ministry of Education, Science, Research and Technology (Projects NATMAR, 03F0198 and MONA 03FO229A). We thank Drs Cynan Ellis-Evans, Kai Bischof, Suzanne Fredericq and Anne-Lise Etienne for their helpful and constructive comments.

References

Bischoff-Bäsmann, B. & Wiencke, C. 1996. Temperature requirements for growth and survival of Antarctic Rhodophyta. *Journal of Phycology*, **32**, 525–535.

Clarke, A., Holmes, L.J. & White, M.G. 1988. The annual cycle of temperature, chlorophyll and major nutrients at Signy Island, South Orkney Islands, 1969–82. *British Antarctic Survey Bulletin*, No. 80, 65–86.

Clayton, M.N. 1994. Evolution of the Antarctic marine benthic algal flora. *Journal of Phycology*, **30**, 897–904.

Cormaci, M., Furnari, G. & Scammacca, B. 1992. The benthic alga flora of Terra Nova Bay (Ross, Sea, Antarctica). *Botanica Marina*, **35**, 541–552.

Drew, K.H. & Hastings, R.M. 1992. A year-round ecophysiological study of *Himantothallus grandifolius* (Desmarestiales, Phaeophyceae) at Signy Island, Antarctica. *Phycologia*, **31**, 262–277.

Eggert, A. & Wiencke, C. 2000. Adaptation and acclimation of growth and photosynthesis of five Antarctic red algae to low temperatures. *Polar Biology*, **23**, 609–618.

Figueroa, F.L. 2002. Bio-optical characteristics of Gerlache and Bransfield Strait waters during an Antarctic summer cruise. *Deep Sea Research II*, **49**, 675–691.

Gain, L. 1912. La flore algologique des régions antarctiques et subantarctiques française. *In* Charcot, J., *ed. Deuxième Expedition Antarctique Francaise (1908–1910)*, *Sciences Naturelles*, *Documents scientifiques*, 1–218.

Gomez, I. & Wiencke, C. 1996. Seasonal growth and photosynthetic performance of the Antarctic macroalga *Desmarestia menziesii* (Phaeophyceae) cultivated under fluctuating Antarctic daylengths. *Botanica Acta*, **109**, 1–7.

Gomez, I. & Wiencke, C. 1998. Seasonal changes in C, N and major organic compounds and their significance to morpho-functional processes in the endemic Antarctic brown alga *Ascoseira mirabilis*. *Polar Biology*, **19**, 115–124.

Gomez, I., Thomas, D.N. & Wiencke, C. 1995a. Longitudinal profiles of growth, photosynthesis and light independent carbon fixation in the Antarctic brown alga *Ascoseira mirabilis*. *Botanica Marina*, **38**, 157–164.

Gomez, I., Wiencke, C. & Weykam, G. 1995b. Seasonal photosynthetic characteristics of *Ascoseira mirabilis* (Ascoseirales, Phaeophyceae) from King George Island, Antarctica. *Marine Biology*, **123**, 167–172.

Gomez, I., Weykam, G., Klöser, H. & Wiencke, C. 1997. Photosynthetic light requirements, metabolic carbon balance and zonation of sublittoral macroalgae from King George Island (Antarctica). *Marine Ecology Progress Series*, **148**, 281–293.

Gordon, A.L. & Molinelli, E.J. 1982. *Southern Ocean Atlas: thermohaline chemical distributions and the atlas data set*. New York: Columbia University Press, 233 plates

KAIN, J.M. 1982. The reproductive phenology of nine species of Rhodophyta in the subtidal region of the Isle of Man. *British Phycological Journal*, **17**, 321–331.

KAIN, J.M. 1987. Photoperiod and temperature as triggers in the seasonality of *Delesseria sanguinea*. *Helgoländer Meeresuntersuchungen*, **41**, 355–370.

KAIN, J.M. 1989. The seasons in the subtidal. *British Phycological Journal*, **24**, 203–215.

KLÖSER, H., FERREYRA, G., SCHLOSS, I., MERCURI, G., LATURNUS, F. & CURTOSI, A. 1993. Seasonal variation of algal growth conditions in sheltered Antarctic bays: the example of Potter Cove (King George Island, South Shetlands). *Journal of Marine Systems*, **4**, 289–301.

KORNMANN, P. & SAHLING, P.-H. 1977. Meeresalgen von Helgoland. Benthische Grün-, Braun- und Rotalgen, *Helgoländer wissenschaftliche Meeresuntersuchungen*, **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, I.M. & ZIMMERMAN, M.H. 1977. Benthic marine algae of the Antarctic Peninsula. *Antarctic Research Series*, **23**, 129–229.

LÜDER, U.H. 2001. Acclimation of photosynthesis and pigments to seasonally changing light conditions in the endemic Antarctic red macroalga *Palmaria decipiens*. *Polar Biology*, **24**, 598–603.

LÜDER, U.H., WIENCKE, C. & KNOETZEL, J. 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. *Journal of Phycology*, **38**, 904–913.

LÜNING, K. 1980a. Critical levels of light and temperature regulating the gametogenesis of three *Laminaria* species (Phaeophyceae). *Journal of Phycology*, **16**, 1–5.

LÜNING, K. 1980b. Control of algal life-history by daylength and temperature. *In* PRICE, J.H., IRVINE, D.E.G. & FARNHAM, W.F., *eds*. *The shore environment*, *vol. 2. Ecosystems*. London: Academic Press, 915–945.

LÜNING, K. 1990. *Seaweeds – their environment*, *biogeography and ecophysiology*. New York: John Wiley & Sons, 527 pp.

LÜNING, K. 1991. Circannual rhythm in a brown alga *Pterigophora californica*. *Botanica Acta*, **104**, 157–162.

LÜNING, K. 1993. Environmental and internal control of seasonal growth in seaweeds. *Hydrobiologia*, **260/261**, 1–14.

LÜNING, K. & TOM DIECK, I. 1989. Environmental triggers in algal seasonality. *Botanica Marina*, **32**, 389–397.

LÜNING, K. & DRING, M.J. 1979. Continuous underwater light measurements near Helgoland (North Sea) and its significance for characteristic light limits in the sublittoral region. *Helgoländer wissenschaftliche Meeresuntersuchungen*, **32**, 403–424.

MANN, K.H. 1982. *Ecology of coastal waters. A systems approach*. Oxford: Blackwell Scientific Publications, 322pp.

RICKER, R.W. 1987. *Taxonomy and biogeography of Macquarie Island seaweeds*. London: British Museum, 344 pp.

SKOTTSBERG, C. 1953. On two collections of Antarctic marine algae. *Arkiv för Botanik*, *Serie 2*, **2**, 531–566.

SOMMER, U. 1998. *Biologische Meereskunde*. Berlin: Springer, 475 pp.

STEIN, J.R. 1973. *Handbook of phycological methods*, *culture methods and growth measurements*. Cambridge: Cambridge University Press, 448 pp.

TOM DIECK, I. 1991. Circannual growth rhythm and photoperiodic sorus induction in the kelp *Laminaria setchellii* (Phaeophyta). *Journal of Phycology*, **27**, 341–350.

WEYKAM, G. & WIENCKE, C. 1996. Seasonal photosynthetic performance of the endemic Antarctic alga *Palmaria decipiens* (Reinsch) Ricker. *Polar Biology*, **16**, 357–361.

WEYKAM, G., THOMAS, D.N. & 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.

WEYKAM, G., GOMEZ, I., WIENCKE, C., IKEN, K. & KLÖSER, H. 1996. Photosynthetic characteristics and C:N ratios of macroalgae from King George Island (Antarctica). *Journal of Experimental Marine Biology and Ecology*, **204**, 1–22.

WIENCKE, C. 1990a. Seasonality of brown macroalgae from Antarctica - a long term culture study under fluctuating Antarctic daylengths. *Polar Biology*, **10**, 589–600.

WIENCKE, C. 1990b. Seasonality of red and green macroalgae from Antarctica - a long-term culture study under fluctuating Antarctic daylengths. *Polar Biology*, **10**, 601–607.

WIENCKE, C. 1996. Recent advances in the investigation of Antarctic macroalgae. *Polar Biology*, **16**, 231–240.

WIENCKE, C., CLAYTON, M. & LANGREDER, C. 1996. Life history and seasonal morphogenesis of the endemic Antarctic brown alga *Desmarestia anceps* Montagne, *Botanica Marina*, **39**, 435–444.

WIENCKE, C. & CLAYTON, M. 2002. *Biology of Antarctic macroalgae*. Rugell/Lichtenstein: Gantner Verlag KG, 239 pp.

WIENCKE, C. & FISCHER, G. 1990. Growth and stable carbon isotope composition of cold-water macroalgae in relation to light and temperature. *Marine Ecology Progress Series*, **65**, 283–292.

WIENCKE, C., RAHMEL, J., KARSTEN, U., WEYKAM, G. & KIRST, G.O. 1993. Photosynthesis of marine macroalgae from Antarctica: light and temperature requirements. *Botanica Acta*, **106**, 78–87.

WIENCKE, C. & TOM DIECK, I. 1989. Temperature requirements for growth and temperature tolerance of macroalgae endemic to the Antarctic region. *Marine Ecology Progress Series*, **54**, 189–197.

WIENCKE, C. & TOM DIECK, I. 1990. Temperature requirements for growth and survival of macroalgae from Antarctica and southern Chile. *Marine Ecology Progress Series*, **59**, 157–170.

WIENCKE, C., RAHMEL, J., KARSTEN, U., WEYKAM, G. & KIRST, G.O. 1993. Photosynthesis of marine macroalgae from Antarctica: light and temperature requirements. *Botanica Acta*, **106**, 78–87.

WYNNE, M.J. 1982. Pbservations on four species of Delesseriaceae (Rhodophyta) from the South Sandwich Islands, the Antarctic. *Contribution from the University of Michigan Herbarium*, **15**, 325–337.