Life strategy and ecophysiology of Antarctic macroalgae

Lebensstrategie und Ökophysiologie mariner Braunalgen der Arktis

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ABBREVIATIONS

α (alpha)	Inital slope of the photosynthetic *vs* light curve. Indicates the photosynthetic efficiency at limiting irradiances
ATP	Adenosine triphosphate
ANOVA	Analysis of Variance
C	Carbon
^{14}C	Radioactive carbon isotope
^{13}C,^{12}C	Stable carbon isotopes
$^{12}C/^{13}C$	Stable isotope ratio
Chl *a*	Chlorophyll *a*
C/N ratio	Quotient between the carbon and nitrogen content
CO_2	Carbon dioxide
$\delta\ ^{13}C$	Carbon isotope composition expressed in % PDB (Bellemnite) (Pee Dee Formation)
DMF	N, N-dimethyl formamide
DMSO	Dimethylsulfoxide
DW	Dry weight
F-values	Coefficient of Fisher defining the ratio between the group and intra-group variances
FW	Fresh weight
G	Gametophytes
HCO_3	Bicarbonate
HCl	Hydrochloric acid
H_{comp}	Number of hours per day at which algae are exposed to compensating irradiances for photosynthesis
H_{sat}	Number of hours per day at which algae are exposed to saturating irradiances for photosynthesis
I_c	Compensation irradiance for photosynthesis or growth
I_k	Saturation irradiance for photosynthesis or growth
L:D	Light regime indicating the number of hours under at which algae are exposed to light or darkness
LSD	Least significant difference (test of multicomparison of means)

N	Nitrogen
NADP	Nicotinamide-adenine dinucleotide phosphate, oxidized
$NaHC0_3$	Sodium bicarbonate
NaOH	Sodium hydroxide
Net P_{max}	Light saturated net photosynthesis
NO_3	Nitrate
NS	Non-reproductive sporophytes
O_2	Oxygen
PEP-CK	Phosphoenolpyruvate carboxykinase
P-I curve	Photosynthesis *vs* irradiance curve
P/R ratio	Quotient between the net photosynthesis and the dark respiration rate
r	Correlation coefficient
r^2	Coefficient of determination
RS	Reproductive sporophyte
RUBISCO	Ribulose- 1,5- bisphosphate carboxylase oxygenase
Tris-Buffer	Tris (hydroxymethyl)-aminomethane
TSC	Thallus specific carbon content
UST	Upper survival temperature
YS	Young sporophytes

ABSTRACT

The present report summarizes the results from a series of publications dealing with eco-physiology of Antarctic marine macroalgae, with particular reference to brown algae. In order to characterize metabolic activity, growth, photosynthetic activity, carbon assimilation and allocation of organic compounds were determined using cultured and field plants of selected species. Data are examined with respect to morpho-functional characteristics, seasonality and depth zonation and are compared with related subjects from previous surveys. To put this information into a perspective, a general overview of the future topics of investigation is briefly outlined at the end of each chapter.

Morphological structure and patterns of biomass allocation along the thallus are major factors affecting macroalgal metabolism. In the perennial endemic Antarctic *Ascoseira mirabilis*, whose strap-like lamina resembles those of *Laminaria* species, meristematic activity and thallus elongation start in late winter-spring leading to a gradient in tissues with different age and physiological properties. O_2-based net photosynthesis (net P_{max}) is higher in the middle regions of the blade than in the growing basal and oldest distal regions. Such a longitudinal profile can be related to ontogenetic development, i. e. photosynthetic O_2 production rates increase directly with tissue development reaching a maximum, then decreasing with further ageing. Age and size of the whole plant affect the magnitude of the photosynthetic activity, but do not alter the longitudinal profiles in Net P_{max} and α. This suggests both a decrease in the metabolic activity with age and changes in the light absorption characteristics with increasing biomass.

Like in *Laminaria* species, light carbon fixation, photosynthetic efficiency (α) and dark respiration increase towards the distal blade regions revealing that these parameters are less susceptible to senescence than is photosynthetic oxygen production. However, light independent carbon-fixation substantially increases towards the oldest distal regions in *Ascoseira mirabilis*. This result contrasts

with the longitudinal variations reported for *Laminaria* or *Fucus*, whose highest dark carbon fixation rates and activities of the enzyme phosphoenolpyruvate carboxykinase (PEP-CK; ß carboxilation) are localized in young growing tissues.

Many Antarctic macroalgae synchronize their reproductive processes to cope with the seasonal variations in daylengths. In algae exhibiting a heteromorphic life-history, the development of small gametophytes and large sporophytes is seasonally determined and involves different physiological adaptations. In members of the order Desmarestiales, reproductive events such as gametogenesis, fertilization and development of early stages of sporophytes take place under dim light in winter, while adult sporophytes grow in late-winter spring. Gametophytes and small stages of sporophytes of *Desmarestia menziesii* are shade adapted organisms with a higher photosynthetic efficiency, a higher content of photosynthetically active pigments per unit weight, and significantly lower saturation (I_k) points for photosynthesis than adult sporophytes. Like in *Ascoseira mirabilis*, the physiological differentiation in the distinct life-history stages of *Desmarestia menziesii* show a relation between light requirements for photosynthesis and morphological characteristics. Growth of small gametophytes and early sporophytes is not constrained at low irradiances in virtue of their small size, high surface area/volume ratios and low proportion of non-photosynthetic tissues, whereas substantially greater inputs of irradiance are required to support metabolism in large and morphologically complex adult sporophytes.

Long-term culture studies using seasonally fluctuating daylengths reveal that growth of Antarctic macroalgae follows two major seasonal patterns. Species denominated "season responders" exhibit an opportunistic life strategy and develop under favourable enviromental conditions. A second group, the so-called "season anticipators", grow and reproduce following a programmed seasonal pattern triggered by daylength regimes, i. e. vegetative growth ocurrs under increasing daylengths in late winter-spring and decreases again in

summer. The physiological bases of these changes are a high net P_{max} and photosynthetic efficiency, accompanied of increasing pigment contents during September and December. In species such as *Ascoseira mirabilis*, *Himantothallus grandifolius* and *Desmarestia menziesii*, elevated respiration rates are a common characteristic and reflect the active biomass formation during this short period. The increased respiratory activity leading to low (or negative) metabolic carbon balance appears to be compensated by utilization of storage carbohydrates such as mannitol and laminaran formed during the previous summer period. The complex morpho-functional anatomy of these species and some seasonal relationships between organic constituents and photosynthetic parameters support the idea of a possible use and remobilization of photoassimilates to power metabolic activity.

Based on the high ambient nutrient concentration in Antarctic waters which are reflected by high C and N contents of macroalgae, it is argued that seasonal changes in growth, photosynthetic activity and allocation of organic compounds are basically dependent on daylength conditions. On the other hand, the low light requirements for growth and photosynthesis determined in these species are interpreted as an adaptation allowing perennial sporophytes to withstand seasonal factors such as ice-cover in winter, phytoplankton blooms in spring and turbid melt-water in summer.

Low compensation and saturation points for growth and photosynthesis set the depth distribution limits of several Antarctic macroalgae. In general, dominant brown algae and understory red algae do not show photoacclimatation with depth being able to photosynthesize at depths of up to 30 m. However, depth dependent shortenings of daily periods for which plants are exposed to irradiances enough to saturate photosynthesis (H_{sat}) cause a decrease in metabolic carbon balances (daily P/R ratios) and consequently in primary productivity.

Finally, the results compiled here confirm that Antarctic macroalgae growing at water temperatures close to 0 °C are able to photosynthesize at rates

comparable to those of macroalgae from temperate latitudes. This ability clearly accounts for the high productivity and abundance of macroalgae in the Antarctic shallow waters.

ZUSAMMENFASSUNG

Die vorliegende Arbeit faßt die Ergebnisse einer Reihe von Publikationen zusammen, die sich mit der Ökophysiologie mariner Makroalgen der Antarktis unter besonderer Berücksichtigung der Braunalgen befassen. Zur Charakterisierung der Stoffwechselaktivitäten wurden sowohl bei ausgesuchten kultivierten Arten als auch bei Pflanzen aus dem Freiland das Wachstum, die photosynthetische Aktivität, die Kohlenstoff-Assimilation und der Gehalt bestimmter organischer Stoffe im Thallus untersucht. Dabei wurden besonders die morpho-funktionalen Zusammenhänge, sowie die Auswirkungen des jahreszeitlichen Wechsels der antarktischen Tageslänge und des Tiefenvorkommens auf die physiologischen Daten dargestellt und mit ähnlichen Untersuchungen früherer Publikationen verglichen. Am Ende jedes Kapitels wird ein allgemeiner Ausblick auf zukünftige Forschungsaufgaben gegeben.

Thallusstruktur, Thallusentwicklung and Thallus-Anatomie sind die wesentlichen Faktoren, die die photosynthetische Aktivität der Algen bestimmen. Bei der mehrjährigen endemisch *Ascoseira mirabilis*, deren bandartige Phylloide denen der *Laminarien* ähneln, beginnt das Wachstum im späten Winter bis Frühling. Aufgrund dieser Faktoren sind die einzelnen Thallusteile unterschiedlich Alt und haben besondere physiologische Eigenschaften. Die Nettophotosyntheserate (net P_{max}) ist in den mittleren Phylloidteilen höher als in den meristematischen Basal- und den älteren Regionen aus den Phylloidspitzen. Dieses Längsprofil steht in Beziehung zur ontogenetischen Thallusentwicklung: Die Nettophotosynthese steigt direkt mit der Gewebedifferenzierung bis zu einem Maximum im Mittelteil des Phylloids an und sinkt danach mit fortschreitender Alterung wieder ab. Auf diese Weise nimmt die photosynthetische Aktivität mit dem Alter und der Größe des gesamten Thallus ab, aber der Gradient der Photosyntheseaktivität entlang des Phylloids bleibt erhalten. Das bedeutet eine Verringerung des Energiebedarfs für das Wachstum

mit zunehmendem Alter und eine Veränderung der Lichtabsorptionscharakteristik mit zunehmender Biomasse.

Ähnlich wie bei den *Laminaria*arten steigt die photosynthetische Kohlenstoff (^{14}C)-Assimilation, die Photosynthese-Effizienz (α) und die Dunkel-Atmung zur Phylloidspitze hin an, allerdings verändern sich diese Parameter weniger deutlich mit zunehmendem Alter des Gewebes als die photosynthetische Sauerstoffproduktion. Die lichtunabhängige Kohlenstoff-Assimilation (Dunkel-Kohlenstoff-fixierung) ist in den ältesten distalen Regionen von *Ascoseira mirabilis* am größten. Dies steht im Gegensatz zu den Befunden an *Laminaria* oder *Fucus*, bei denen die höchsten Raten der lichtunabhängigen Kohlenstoffixierung und die höchsten Aktivitäten des Enzyms Phosphoenolpyruvat Carboxykinase (PEP-CK) in jungen, wachsenden Geweben auftreten.

Viele antarktische Makroalgen synchronisieren ihre Reproduktionsprozesse an die jahreszeitlich variierenden Tageslichtlängen. In Algen mit einem heteromorphen Lebenszyklus ist die Entwicklung vom mikroskopisch kleinen Gametophyten zum großen Sporophyten jahreszeitlich bestimmt. Jedes Entwicklungstadium weist besondere physiologische Eigenschaften auf. Bei den Arten der Ordnung Desmarestiales finden Gametogenese, Befruchtung und Bildung junger Sporophyten während der winterlichen Dämmerungsphase statt, während die ausgewachsenen Sporophyten im späten Winter bis Frühling wachsen. Es wurde gezeigt, daß die Gametophyten und die jungen Stadien der Sporophyten von *Desmarestia menziesii* an Schwachlicht angepaßt. Sie weisen eine höhere Photosynthese-Effizienz, einen höheren Gehalt an photosynthetisch aktiven Pigmenten pro Gewichtseinheit und signifikant niedrigere Lichtsättigungspunkte (I_k) in der Photosynthese auf als ausgewachsene Sporophyten. Wie bei *Ascoseira mirabilis* zeigt sich bei den verschiedenen Stadien im Lebenszyklus von *Desmarestia menziesii* eine ähnlicher Zusammenhang zwischen dem Lichtbedarf für die Photosynthese und Thallusstruktur. Das Wachstum der Gametophyten und

jungen Sporophyten ist aufgrund eines geringen Größe, einem hohen Verhältnisses von Oberfläche zu Volumen und eines geringen Anteils von nicht photosynthetisch aktivem Gewebe auch im Schwachlicht möglich. Dagegen sind höhere Bestrahlungsstärken erforderlich, um Stoffwechsel und Wachstum der großen und morphologisch komplexen Sporophyten ausreichend zu gewährleisten.

Langzeitstudien an Kulturen unter simulierten antarktischen Tageslängen zeigen deutlich, daß das Wachstum der antarktischen Makroalgen zwei jahreszeitlichen Hauptmustern folgt. Arten die als "season responders" bezeichnet werden, zeigen eine opportunistische Lebensstrategie und entwickeln sich nur unter für die einzelnen Arten vorteilhaften Lichtbedingungen d.h. unter meist hohen Photonenflußraten. Eine zweite Gruppe, die sogenannten "season anticipators", wachsen und reproduzieren sich nach einem programmierten jahreszeitlichen Muster, das durch die Tageslängenausgelöst wird, d.h. vegetatives Wachstum tritt unter zunehmenden Tageslängen im späten Winter bis Frühling auf und nimmt im Sommer wieder ab. Die physiologische Basis dieses jahreszeitlichen Wachstumsmuster der "season anticipators" liegt in hohen Nettophotosyntheseraten und hohen Photosynthese-Effizienzen, die während der Monate September bis Dezember von einem anwachsenden Pigmentgehalt gestützt wird. Bei Arten wie *Ascoseira mirabilis*, *Himantothallus grandifolius* und *Desmarestia menziesii* ist die Wachstumsperiode mit einer erhöhten Dunkel-Atmung gekoppelt.

Die erhöhte Atmungsaktivität während der Wachstumsperiode im Spätwinter-Frühling, welche zu niedrigen Photosynthese-Atmung-Verhälnissen führt, scheint durch die Nutzung der Reservestoffe Mannitol und Laminarin ausgeglichen zu werden, die während der vorhergehenden Sommerperiode gebildet werden. Die komplexe morphofunktionelle Anatomie dieser Arten und die Korrelation zwischen Gehalten an organischen Stoffen und Photosyntheseparametern unterstützen die Vorstellung einer möglichen Nutzung

und Remobilisierung der Photoassimilate, um das Wachstum im Frühjahr zu unterstützen.

Aufgrund der hohen Nährstoffkonzentration in den antarktischen Gewässern, die sich in hohen C und N Gehalten der Makroalgen widerspiegeln, wird argumentiert, daß die saisonalen Variationen im Wachstum, der Photosyntheseaktivität und der Verteilung der organischen Verbindungen im wesentlichen von der Tageslänge abhängen. Auf der anderen Seite wird der geringe Lichtbedarf für Wachstum und Photosynthese, der für diese Arten kennzeichnend ist, als eine Anpassung gesehen, die es mehrjährigen Sporophyten ermöglicht, der langandauernden Belastung durch die Eisdecke im Winter, die Phytoplanktonblüte im Frühling und trübes Schmelzwasser im Sommer zu widerstehen.

Geringe Lichtkompensations- und Sättigungspunkte für Wachstum und Photosynthese setzen insbesondere die Grenzen für die Tiefenverteilung verschiedener antarktischer Makroalgen. Im allgemeinen zeigen die vorherrschenden Braunalgen und die "Unterwuchs" Rotalgen keine Photoakklimatisation mit der Tiefe. Netto-Photosynthese ist bis in Tiefen von 30 m möglich. Aber die mit zunehmender Tiefe stärker werdende Einengung der täglichen Zeiten, in denen die Photosynthese lichtgesättigt ist erreicht (H_{sat}), bewirkt abnehmende Kohlenstoffbilanzen (tägliches P/R-Verhältnis) und schränkt so die Primärproduktivität ein.

Schließlich beweisen die hier zusammengestellten Ergebnisse, daß die antarktischen Makroalgen, die bei Wassertemperaturen um 0 °C wachsen, Photosynthese- und Wachstumsraten aufweisen, die denen der Makroalgen gemäßigter Breiten entsprechen. Diese Fähigkeit ist ein weiterer Faktor, der die hohe Produktivität von Makroalgen in den antarktischen Flachgewässern ermöglicht.

1. INTRODUCTION

Brown algae constitute approximately 30 % of the macroalgal taxa described for the Antarctic marine flora (Lamb & Zimmermann 1977), and because of their abundance, large size, and ecological dominance, they account for a great proportion of macroalgal biomass in several Antarctic coastal systems (Moe & Silva 1977, Lamb & Zimmermann 1977, Zielinski 1990, Westermeier et al. 1992, Klöser et al. 1996). A number of SCUBA diving observations and studies on biogeographic distribution provided a bulk of data on species composition, abundance and zonation patterns (Neushul 1961, 1965, Délepine 1966, Zaneveld 1966, Moe & DeLaca 1976, DeLaca & Lipps 1976, Richardson 1979) indicating also that much of the genera of brown algae are monotypic and endemic to the Antarctic region (Knox 1979, Santelices 1989, Lawson 1988, Clayton 1994). Especially remarkable are the diversity and abundance of members of the order Desmarestiales dominating the sublittoral habitats of the Antarctic Peninsula and adjacent islands such as King George Island (South Shetland Islands) and Signy Island (South Orkney Islands), documented by Lamb & Zimmermann (1977), Zielinski (1990), Brouwer et al. (1995), Klöser et al. (1994, 1996).

Studies focused on the eco-physiology of Antarctic macroalgae began relatively late. Up to the end of the 80's less than 10 publications on physiology of Antarctic brown algae were available. Drew (1977) described photosynthesis and respiration in *Ascoseira*, *Desmarestia* and *Himantothallus* from populations located in Signy Island, South Orkney Islands. This author concluded that these species do not exhibit "*obvious adaptations to the extreme conditions of their environment,... having photosynthesis and respiration rates similar to winter-adapted temperate species*". In this context, a particular emphasis was placed on the physiology of *Himantothallus grandifolius* including seasonal *in situ* studies on growth, photosynthesis and carbon balance related to some environmental factors, i. e. nutrients, ice-cover regime and light conditions (Drew & Hastings 1992). Other investigations during this period were centered in the area of Admiralty

Bay, King George Island, where *Adenocystis utricularis* and *Himantothallus* were examined in relation to their photosynthetic capacity, pigment contents and organic contents (Czerpak et al. 1981, Gutkowski & Maleszewski 1989). The first studies concerning morphogenesis and reproductive life history were conducted in *Desmarestia* spp (Moe & Silva 1977, 1989), *H. grandifolius* (Moe & Silva 1981) and *Ascoseira mirabilis* (Moe & Henry 1982) and provided preliminary insights into the life history of Antarctic macroalgae. On the basis of these observations, the number of investigations addressing ecological and physiological processes of Antarctic macroalgae increased significantly during the last six years. Improvements in the techniques of isolation and cultivation of macroalgae as well as the use of simulated environmental conditions in the laboratory allowed important advances in the knowledge of seasonal growth and reproductive patterns. Temperature requirements for growth and survival of different species were primarily documented by Wiencke & tom Dieck (1989, 1990). These authors demonstrated that sporophytes of the endemic species *Ascoseira mirabilis*, *Phaeurus antarcticus*, *Desmarestia anceps* or *Himantothallus grandifolius* grow from 0 up to 5-10 °C with an upper survival temperature (UTS) between 11 and 13 °C. Such UST's are significantly lower than those determined for cold-temperate species from South Chile (Wiencke & tom Dieck 1990) or *Laminaria* species from the Northern Hemisphere (Bolton & Lüning 1982). The second aspect that called special attention was the effect of light conditions on growth and reproduction (see Wiencke 1990a,b), especially light requirements for growth and completion of life-cycle as well as the development of different generations in species with a heteromorphic life-history. It is now known that various of the reproductive events and life history events in Antarctic macroalgae are seasonally determined: microscopic gametophytes and early stages of sporophytes in *Desmarestia* (Wiencke et al. 1991, 1995, 1996), *Himantothallus* (Wiencke & Clayton 1990) and *Phaeurus antarcticus* (Clayton & Wiencke 1990) grow under limited light conditions during winter, whereas growth of adult sporophytes is restricted to late winter-spring. In culture studies under simulated fluctuating

Antarctic daylength it was possible to demonstrate that growth of macroalgae follows two different strategies to cope with the strong seasonality of the light regime in the Antarctic. "Season responder" species exhibit an opportunistic strategy growing only under optimal light conditions mainly in summer, whereas a second group so-called "season anticipators" develop under a seasonally programmed pattern, which does not strongly depend on irradiance levels. These species mostly grow and reproduce in winter and spring.

Such findings raised further questions on the effect of temperature and light conditions on photosynthetic metabolism. The hypothesis that low temperature and low light requirements for growth of Antarctic macroalgae are based on adaptations in carbon metabolism, especially photosynthesis, was particularly addressed. Preliminary screenings on selected Antarctic especies, particularly brown algae, revealed that photosynthetic rates and respiration measured at 0 °C are comparable to rates of macroalgae from temperate regions (Thomas & Wiencke 1991). Moreover, Antarctic species exhibited very low light requirements for photosynthesis (Wiencke et al. 1993). Later, more detailed studies focussing on physiology of red algae revealed seasonal changes in photosynthetic performance and light requirements for photosynthesis (Weykam 1996, Weykam & Wiencke 1996). In the light of this evidence, it was possible to argue that macroalgae are effectively highly adapted to the Antarctic environment. However, the general conclusion emerging from these investigations showed the need of further studies on morpho-functional aspects, on the relationship between growth and photosynthesis on a seasonal basis as well as on internal and external factors affecting photosynthesis and productivity of Antarctic macroalgae (Kirst & Wiencke 1995, Wiencke 1996). In this context, the studies compiled here constitute one of such efforts and add new insights into the physiological life strategy of brown algae.

2. OBJECTIVES

The investigations were basically focused on growth and photosynthetic metabolism of selected brown algae using cultured and field plants. The following main aspects were considered:

1. To determine the effects of seasonality of Antarctic light conditions on the photosynthetic characteristics of macroalgae, growth rates, photosynthetic performance and pigment contents were measured in the brown algae *Ascoseira mirabilis* and *Desmarestia menziesii* cultivated under simulated fluctuating Antarctic daylengths.

2. To compare the responses of the culture material with the situation in plants growing under natural conditions, photosynthetic characteristics were measured in macroalgae collected directly from the field at King George Island between September 93 and February 94. These plants were also used in determinations of organic compounds such as carbon and nitrogen, proteins, amino acids, storage carbohydrates, etc. Data were related to the seasonal variations in photosynthesis.

3. The investigations in *Ascoseira mirabilis* basically address questions on morphological structure, biomass allocation, age and size of the thallus and their significance to the photosynthetic characteristics. Using photosynthesis data from culture and field material and ^{14}C-assimilation studies in culture plants, a morpho-functional model is proposed.

4. The physiological characteristics of different generations in species with a heteromorphic life history were studied in *Desmarestia menziesii*. The hypothesis that development of small gametophyes and young stages of sporophytes under dim light in winter is the result of adaptations at the

photosynthetic level was tested comparing their photosynthetic performance, pigment contents and light requirements for photosynthesis with those of adult sporophytes.

5. Light availability as a determining factor for depth zonation of Antarctic macroalgae was addressed in two brown algae, *Himantothallus grandifolius* and *Desmarestia menziesii*, and three red algae, *Palmaria decipiens*, *Kallymenia antarctica*, and *Gigartina skottbergii* from sublittoral populations at Potter Cove (King George Island). *In situ* irradiance data, photosynthetic performance, light requirements for photosynthesis, as well as C, N, and pigment contents were used to estimate metabolic carbon balance, photoacclimation and other physiological adaptations in plants growing at depths between 10 and 30 m.

6. Finally, in order to integrate data and generate an overview of the photosynthetic variation in the whole macroalgal community, a screening study examining the physiological characteristics of 36 brown, red and green macroalgae commonly found at King George Island was performed.

3. EXPERIMENTAL APPROACH AND METHODOLOGICAL CONSIDERATIONS

3.1. Algal material

The algal species examined in this study were collected in King George Island, South Shetlands. Two species, *Ascoseira mirabilis* Skottsberg and *Desmarestia menziesii* J. Agardh were analysed in detail:

1. ***Ascoseira mirabilis***: This endemic Antarctic species is the only member of the order Ascoseirales and is characterized by a complex morphology and anatomy resembling some *Laminaria* species but has fucalean like-life history, i. e. this species lack a free living gametophyte. Despite these highly derived attributes, this alga exhibits isogamy as fertilization mechanism, often found in lower systematic categories of brown algae (Clayton 1987, Clayton & Ashburner 1990, Müller et al. 1990). The species commonly inhabits the shallow coastal waters of the Antarctic Peninsula and adjacent islands (Lamb & Zimmermann 1977) and coexists with the large Desmarestiales in flat or weakly inclinated platforms at depths generally ≥ 15 m (Zielinski 1990, Klöser et al. 1994, 1996)

2. ***Desmarestia menziesii***: Like *Ascoseira mirabilis*, this species occurs in the Antarctic Peninsula and adjacent islands (Lamb & Zimmermann 1977), however, northern populations have also been reported to occur in south Atlantic islands (Falkland Islands, Papenfuss 1964) making its status as an endemic Antarctic species controversial. The life history of *Desmarestia menziesii* is heteromorphic with dioecious microscopic gametophytes and large sporophytes (Wiencke et al. 1995). In the sublittoral at King George Island, this species is together with *Desmarestia anceps* and *Himantothallus grandifolius* generally the dominant organism in macroalgal assemblages between 5 and 20-25 m depth (Klöser et al. 1996). Apparently, substrate characteristics, water turbulence (Klöser et al. 1994, 1996), and grazing

pressure (Iken 1996, Iken et al. 1997) are the major competitive factors between these species.

The other brown algal species, *Himantothallus grandifolius* (A. et E. S. Gepp) Zinova and *Desmarestia anceps* Montagne and the red algae *Palmaria decipiens* (Reinsch) Ricker, *Kallymenia antarctica* Hariot and *Gigartina skottbergii* (Bory) Setchell et Gardner used for comparisons in studies on depth variation have been described in detail by Lamb & Zimmermann 1977, Wiencke & Clayton (1990), Drew & Hastings (1992), Weykam (1996) and Wiencke et al. (1996).

Table 1 shows the experimental design and the species used accordingly. Culture material of *Ascoseira mirabilis* and *Desmarestia menziesii* used for growth, O_2-based photosynthesis, ^{14}C-assimilation, and pigment contents was originally isolated as spores/zygotes from macroalgal assemblages located near the Marsh Station during the Antarctic summers 1985-86 and transported to the laboratory at the Alfred Wegener Institute in Bremerhaven (Clayton & Wiencke 1986).

Table 1. Experimental schedule indicating the species and main aspects examined

SPECIES	STUDIES PERFORMED					
	Growth	Photosynthesis		Pigments	C-N analysis	Organic compounds
		O_2	^{14}C			
LABORATORY						
Ascoseira mirabilis	$X^{a,b}$	$X^{a,b}$	$X^{a,b}$	$X^{a,b}$		
Desmaresia menzeisii	X^{a}	X^{a}		X^{a}	X^{a}	
FIELD						
Chlorophyta						
Enteromorpha bulbosa		X		X	X	
Monostroma hariotii		X		X	X	
Urospora penicilliformis		X		X	X	
Chrysophyta						
Antarctosaccion applanatum		X		X	X	

Continuation **Table 1**

SPECIES	PERFORMED STUDIES				
	Growth	Photosynthesis		Pigments	C-N analysis	Organic compounds
		O_2	^{14}C			
Phaeophyta						
Adenocystis utricularis		X^{a}		X^{a}	X^{a}	X^{a}
Ascoseira mirabilis		$X^{a.b}$		$X^{a.b}$	$X^{a.b}$	$X^{a.b}$
Cystosphaera jacquinotii		X		X	X	
Desmarestia anceps		$X^{a.c}$		$X^{a.c}$	$X^{a.c}$	
Desmarestia antarctica		X^{a}		X^{a}	X^{a}	
Desmarestia menziesii		X^{a}		X^{a}	X^{a}	X^{a}
Geminocarpus geminatus		X		X	X	
Halopteris obovata		X^{a}		X^{a}	X^{a}	
Himantothallus grandifolius		$X^{a.c}$		$X^{a.c}$	$X^{a.c}$	
Phaeurus antarcticus		X^{a}		X^{a}	X^{a}	
Rhodophyta						
Ballia callitricha		X		X	X	
Callophyllis variegata		X		X	X	
Callophyllis sp.		X		X	X	
Curdiea racovitzae		X^{a}		X^{a}	X^{a}	
Delesseria lancifolia		X		X	X	
Georgiella confluens		X		X	X	
Gigartina skottsbergii		X^{c}		X^{c}	X^{c}	
Gymnogongrus antarcticus		X		X	X	
Hymenocladiopsis crustigena		X		X	X	
Iridaea cordata		X^{a}		X^{a}	X^{a}	
Kallymenia antarctica		$X^{a.c}$		$X^{a.c}$	$X^{a.c}$	
Myriogramme mangini		X		X	X	
Myriogramme smithii		X		X	X	
Palmaria decipiens		$X^{a,c}$		$X^{a,c}$	$X^{a,c}$	
Pantoneura plocamioides		X		X	X	
Phycodrys quercifolia		X		X	X	
Phyllophora ahnfeltioides		X		X	X	
Phyllophora appendiculata		X		X	X	
Picconiella plumosa		X^{a}		X^{a}	X^{a}	
Plocamium cartilagineum		X^{c}		X^{c}	X^{c}	
Porphyra endiviifolium		X		X	X	
Unidentified species		X		X	X	

[a] : Seasonal basis; [b] : intra-thallus variation; [c] : depth variation

The field plants were collected during spring-summer 1993-94 in Potter Cove (Dallmann Laboratory-Jubany Station) and were used immediatedly for photosynthetic measurements and Chl *a* determinations. For determinations of C and N contents, proteins, amino acids and storage carbohydrates, samples were firstly lyophilized (Lyovac GT 2, Finn.Aqua), transported to the laboratory in Bremerhaven and kept at room temperature until later analysis. Further details of the algal collection and sample treatments are described in Gómez et al. 1995, 1996, Gómez & Wiencke 1997.

3.2. Algal cultivation under fluctuating Antarctic daylength as a tool for simulation of seasonal development

In general, field studies in Antarctic environments are hampered by considerable logistic difficulties, especially when physiological variables shall be examined on a seasonal basis. Therefore it was decided to do a major part of the work using cultivated specimens. The use of culture material for physiological purposes may also be preferable, especially if factors such as age of plants or timing of reproductive events are investigated. Moreover, cultured plants growing under controlled nutrient supply and irradiance allow a more accurate comparison of metabolic responses. Effects linked to individual variability *vs* ambient interaction can be studied more easily. The exposure of the algae to simulated fluctuating Antarctic daylengths has revealed to be advantageous in studies on seasonal growth and reproduction of Antarctic macroalgae. Other environmental variables in the Antarctic (nutrients, salinity or temperature) are constant throughout the year and, hence, have no or only a slight effect on seasonal development (Wiencke 1990, a,b).

The cultures were kept under light periods varying between 5 h light in winter and 19-20 h light during summer corresponding to the light regime in King George Island. An irradiance of 10 to 13 µmol photon m^{-1} s^{-1} was provided by cool white fluorescence tubes (Osram L58/W19). Temperature was 0 ± 1 °C (average temperature at King George Island) and nutrients were maintained

always at saturating levels of 0.6 mM nitrate and 0.025 mM phospate. The culture medium (Provasoli enriched seawater, 34 ‰ salinity) was changed every 15 days. These conditions do not limit growth (see Wiencke & tom Dieck 1989, 1990, Wiencke 1990a, b) and will be discussed in detail on the section concerning N contents.

3.3. Determination of growth rates and thallus elongation

Specific growth in plant cultivated under fluctuating daylengths was determined by measuring the increases in fresh weight after 30 days according to the following equation:

$$\text{Specific growth } (\% \, d^{-1}) = \frac{100 \ln(W_t/W_o)}{T}$$

Where W_o is the initial fresh weight, N_t is the fresh weight at day t and T the 30 days interval.

In the particular case of *Ascoseira mirabilis*, patterns of thallus development was measured in five 12-month old plants using the punched-hole method described by Lüning et al. (1973). At the beginning of the growth season, holes of 5 mm diameter spaced each 2 cm were punched along the blade with a cork borer. The displacement of the holes was monitored monthly. When the basal region reached a wide greater than 3 cm, additional holes were made horizontally (**Publication 1**). Determinations of surface area of the blade were made using cut paper tracings of the lamina.

3.4. Oxygen determinations

For photosynthetic measurements, samples were put into closed measuring plexiglass chambers connected to a Clark type O_2 electrodes (Eschweiler and WTW; Gómez et al. 1995a,b). In all cases, O_2 levels were adjusted to 50 % saturation before each measurement. It is known that this O_2 concentration does not inhibit photosynthetic performance of macroalgae (Bidwell & Maclachlan

1985). The medium in the measuring chamber was additionally enriched by 3 mM $NaHCO_3$ and buffered by 8 mM Tris/NaOH (pH 8) to avoid C depletion during the experiment.

An important methodological factor often discussed in this type of studies is the use of thallus pieces or discs. Wounding effects have been regarded as a potential factor adding uncertainty to the photosynthetic data. However, the photosynthetic response of thallus pieces following cuttings appear to be variable and contradictory (Hatcher 1977, Drew 1983). Whereas in algae such as *Macrocystis pyrifera* the use of cutting pieces increases significantly dark respiration causing inaccurate estimates of photosynthesis (Arnold & Manley 1985), in discs of *Laminaria*, wound respiration dissapeared when discs were "aged" in sea water for 12 h (Drew 1983, Bidwell & McLachlan 1985). Due to the morphological similarities with *Laminaria* and the space limitations imposed by the measuring chamber, experimentations with *Ascoseira mirabilis* included always the use of "aged" thallus pieces. Comparative data from "aged" and non-incubated discs (**Table 2**) do not reveal obvious differences in photosynthetic

Table 2. Comparison of photosynthetic parameters from incubated and non-incubated dics cut from adjacent parts of adult *Ascoseira mirabilis* blades from King George Island (spring 1993). Pre-incubated discs were maintained overnight in natural sea water at 0 °C. Units: Net P_{max}, dark respiration and gross photosynthesis in μmol O_2 g^{-1} FW h^{-1}; α in μmol O_2 g^{-1} FW h^{-1} (μmol photon m^{-2} s^{-1})$^{-1}$ and I_c and I_k in μmol photon m^{-2} s^{-1}.

Parameters	Pre-incubated		Non-incubated		Mean	St. dev	% Error
	I	II	III	IV			
Net P_{max}	22.41	30.55	21.02	27.92	25.48	3.90	15.32
Respiration	-2.85	-3.07	-4.39	-1.91	-3.06	0.88	29.01
Gross P_{max}	25.27	33.63	25.41	29.83	28.54	3.46	12.14
α	1.54	1.25	1.48	1.26	1.38	0.13	9.37
I_c	1.64	1.68	1.88	0.99	1.55	0.33	21.66
I_k	16.17	26.13	16.02	23.05	20.34	4.38	21.55

performance or an enhancement of dark respiration in *Ascoseira mirabilis*. On the other hand, samples from cultured *Desmarestia menziesii* material were measured immediately. This was possible because wounding effects are much

lower due to the branched thallus structure compared to the leathery *Ascoseira mirabilis*.

3.5. Determination of photosynthetic parameters

Before determination of photosynthesis, respiratory activity was measured after exposure of 20 min to darkness. The samples were then consecutively exposed to increasing irradiances from 1 to approx. 800 µmol photon m^{-2} s^{-1} for 10 min each. It must be emphazised that limiting (1, 3, 5, 10 and 27 µmol photon m^{-2} s^{-1}) and saturating (200, 250, 300, 400, 600 and 800 µmol photon m^{-2} s^{-1}) irradiances allowed relatively reliable curve fitting and parameter calculations (Henley 1993). In this sense, exposures of ≤ 10 min to each irradiance avoided photoinhibition.

The photosynthetic parameters determined in this study were: saturated net photosynthesis (net P_{max}), photosynthetic efficiency (α), dark respiration and compensation (I_c) and saturation (I_k) points of photosynthesis. Two different methods were used for calculation of these parameters. The first method was used in Gómez et al. 1995a,b, 1996, Gómez & Wiencke 1996, 1997 and consisted of a simple interpolation of points along the P-I curve. P_{max} was calculated as the average of O_2 production in the saturation region between 200 and 800 µmol photons m^{-2} s^{-1} and α, was determined as the slope in the linear region of the curve at low irradiances (1 to 27 µmol photon m^{-2} s^{-1}). In the second method (Gómez et al. 1997a,b, Gómez & Wiencke 1997) functions describing non-linear curves were fitted to the data set. Two equations were preferentially used due to their versatility and good fit to the data from macroalgal P-I curves (Nelson & Siegrist 1987, Henley 1993). The first equation describes an exponential curve:

$$P = P_{max} (1 - \exp^{\alpha I/P_{max}}) + R_{cal} \qquad \text{(Webb et al. 1974)}$$

and the second is a hyperbolic tangent function:

$$P = P_{max} \tanh (\alpha I/P_{max}) + R_{cal} \qquad \text{(Jassby \& Platt 1976)}$$

Where P is the gross photosynthesis [range between the intersection with the Y axis and the saturated region of the curve]. P_{max} is the saturated net photosynthesis, tanh is the hyperbolic tangent, I is the irradiance, α is the slope of the linear region and R_{cal} is the estimated dark respiration.

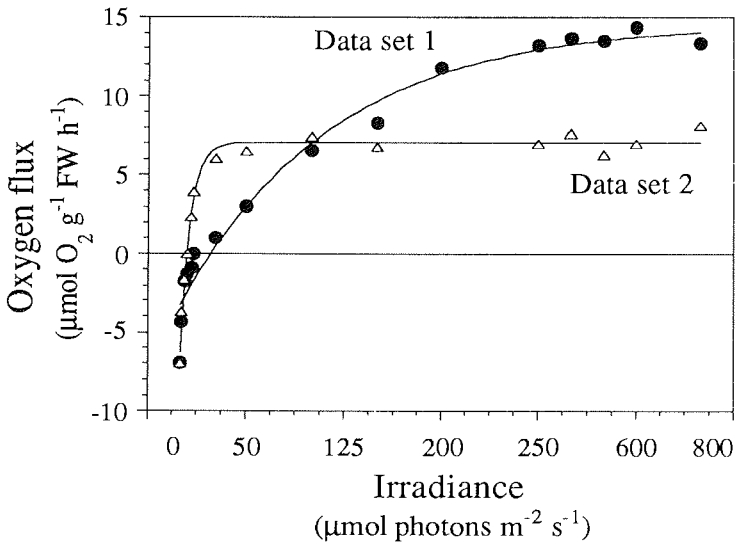

Fig. 1. Example of curve-shape variation in two samples of *Ascoseira mirabilis* measured during the May 1994.

Overall, the P-I curves obtained throughout this study showed different shapes. **Fig. 1** shows two different P-I curves obtained from culture plants of *Ascoseira mirabilis*. These curves are used here to show the variability inherent to the curve shape and its implications for the magnitude of photosynthetic parameters. It is easy to visualize that data set 1 respond more slowly to increasing irradiances than data set 2 and thus photosynthesis is saturated relatively at high irradiances. In contrast, data set 2 shows a very high photosynthetic efficiency at low irradiance (high slope α) and consequently a very low saturation point of photosynthesis.

Table 3 summarizes the differences and similarities in the magnitude of parameters calculated using the methods described above. In general, net P_{max} does not show significant differences between the two methods, however, some

differences in the accuracy of the estimations can be demonstrated. Net P_{max} calculated as the arithmetic average at saturating irradiance shows a relative error of 5.9 % for data set 1, whereas the relative error of net P_{max} was 7.7 % and 6.5 % when exponential and hyperbolic functions, respectively, were used. For data set 2, a simple average of points in the saturation regions attains a relative error close to 9 %, which subtantially decreases using exponential (3.1 %) and tangent hyperbolic (3.4 %) functions.

Table 3. Comparisons of P-I curve parameters estimated using three different methods. Data correspond to photosynthetic measurements carried out in cultured *Ascoseira mirabilis* during May 1994. Standard errors (in parentheses) and relative percentage error (RE) of each method are indicated. Correlation coefficients for linear and non-linear models were significant at 95 % ($r \geq 0.88$ and $r \geq 0.98$, respectively). Units: P_{max} and Dark respiration (R_{cal} and R_{meas}) in μmol O_2 g^{-1} DW h^{-1}; α in μmol O_2 g^{-1} DW h^{-1} (μmol photon m^{-2} s^{-1}).

Parameters	CURVE FIT					
	Arithmetic/linear regression		Exponential		Tangent hyperbolic	
	Data set 1	Data set 2	Data set 1	Data set 2	Data set 1	Data set 2
Net P_{max}	13.30 (0.78)	7.18 (0.63)	14.61 (1.13)	7.00 (0.21)	14.04 (0.91)	6.96 (0.23)
(% RE)	5.90	8.89	7.74	3.08	6.52	3.38
α	0.58 (0.15)	0.97 (0.11)	0.12 (0.01)	0.93 (0.08)	0.09 (0.01)	0.68 (0.05)
(% RE)	26.2	11.39	14.4	8.70	13.25	8.32
R_{cal}	-5.198	-5.466	-3.26 (0.62)	-6.23 (0.48)	-2.93 (0.62)	-5.90 (0.51)
(% RE)	17.19	11.96	19.10	7.84	21.43	8.68
R_{meas}	-6.967	-6.954				

In contrast to net P_{max}, α values varied significantly depending on the method used. For example, linear regressions from data set 1 yielded α values of 5.8 μmol O_2 g_{-1} DW h^{-1} (μmol photon m^{-2} s^{-1})$^{-1}$ (error 26 %) and are significantly higher than those from exponential [0.12 μmol O_2 g^{-1} DW h^{-1} (μmol photon m^{-2} s^{-1})$^{-1}$] or hyperbolic [0.09 μmol O_2 g^{-1} DW h^{-1} (μmol photon m^{-2} s^{-1})$^{-1}$] attaining relative errors of 14.4 and 13.2 %, respectively. For data set 2, linear regression and exponential equation provided similar estimations of α [0.9 μmol

O_2 g^{-1} DW h^{-1} (μmol photon m^{-2} $s^{-1})^{-1}$] with no obvious differences in relative errors. These results are attributed to the convexity of each curve, i. e, the transition region from limiting to saturating irradiance. Exponential curves have a lower convexity than hyperbolic tangent curves and therefore tend to increase α (Henley 1993). The high α values obtained with a linear regression for data set 1 may be due to a the relatively unreliable and noisy characteristics of these data in the region between 1 and 27 μmol photon m^{-2} s^{-1}. Thus, to reach a significant regression coefficient, the slope was calculated eliminating the last point (27 μmol photon m^{-2} s^{-1}) from the light limited region improving the accuracy but significantly overestimating α. Similarly, the low α affected the calculated R_{cal}, defined as the intersection with the Y axis. Under optimal conditions R_{cal} has the same values as measured dark respiration (R_{meas}). The best estimate of R_{cal} for the data set 1 was obtained using a the linear equation (17 % error). In data set 2, where a rapid saturation curve is displayed, R_{cal} was more accurately determined using the exponential function (7.8 %).

This example gives an idea how the magnitude of photosynthetic parameters varies depending on the method used for calculations (Nelson & Siegrist 1987). In general, P-I curves with low α are best fitted with the arithmetic/linear regression method, especially when more accurate R_{cal} is desired. Non-linear equations, by contrast, provide accurate P_{max}, α and R_{cal} from slightly noisy data and a rapidly saturated curve, which is often found for Antarctic macroalgae. Moreover, non-linear equations have normally a very good correlation ($r > 0.98$), whereas linear regressions at the light limited region generally do not exceed $r = 0.95$. The use of less than 5 points in this region necessarily requires a high correlation coefficient to meet significance.

3.6. Determination of ^{14}C-fixation in Ascoseira mirabilis

Rates of carbon assimilation were measured simultaneously with experiments of O_2-based photosynthesis (Gómez et al. 1995a, 1996). Photosynthetic carbon assimilation was determined in sample discs using saturating irradiances of 200

μmol m^{-2} s^{-1} after pre-incubating the sample discs for 15 min at the same irradiance. Algal material pre-incubated in the dark for 30 min was used for light independent carbon fixation. The samples were then incubated for 30 min with 9.1 KBq ^{14}C ml^{-1} as $NaH^{14}CO_3$ (Amersham Buchler GmbH). After incubation, the samples were rinsed in unlabelled media and placed into liquid nitrogen. Samples were then solubilised with 200 µl of perchloric acid (70 %) and 500 µl of hydrogen peroxide (35 %). Radioactivity in the samples was measured in a Packard Tri-Carb 460C liquid scintillation counter adding 5 ml Hionic Fluor scintillation cocktail. Quench corrections were made using an external standard.

3.7. Analysis of pigments

In most of the cases, photosynthesis was also expressed in terms of Chl *a*. Therefore, after determination of photosynthetic oxygen evolution, samples were analysed for determination of pigments. In general, two methods were used. The first method, used for *Ascoseira mirabilis* and *Desmarestia menziesii*, consisted of the extraction of Chl *a*, Chl *c*, fucoxanthin and ß-carotene according to Evans (1988), which is based on three succesive extractions using dimethyl sulfoxide (DMSO), acetone (90%), methanol (80%) and hexane. In the DMSO extract and Acetone-Methanol extract Chl *a*, Chl *c* and fucoxanthin contents were extracted, while ß-carotene was determined from the Acetone-Hexane extract. The extinction of the DMSO extract was measured at 582, 631, 665 nm; Acetone-Methanol extract at 470, 581, 631, 664 nm and Acetone-Hexane extract at 480, 615, 661 nm with a spectrophotometer (Philips, PU-8700: Gómez et al. 1995a, 1996, Gómez & Wiencke 1996). The second method for determination of Chl *a* was based on an extraction with N,N-dimethylformamide (DMF) as described by Inskeep & Bloom (1985). After an incubation period of 3 d at 4 °C in the dark, the extinction was measured in a spectrophotometer (Milton Roy, Spectronic 401) at 664.5 nm for red and brown algae and at 347 and 665 nm for green algae (Gómez et al. 1995b, 1997b, Gómez & Wiencke 1997, Weykam et al. 1996). Both methods give comparable values of Chl *a*.

3.8. Determination of total C and N contents, and stable C isotope composition ($\delta^{13}C$)

For measurement of C and N analysis, the previously lyophilized samples were once more dried at 60 °C for 24 h and finely pulverized. The weight of duplicate sub-samples (approx 1 mg) was determined on a Sartorius supermicro balance. The samples were then put in tin cups and assayed for total N and C (% DW) with a Carlo Erba NA-1500 elemental analyser calibrated with acetanilide ($C_8 H_9 NO$, Carlo Erba).

For the carbon isotope composition, samples were firstly acidified with 0.1 N HCl to eliminate the inorganic carbon and once more freeze-dried in a lyophylizer (Alpha I-5, Martin Christ GmbH & Co.) at 0.02 mb (approx -45 °C) for 48 h. Algal material was transferred to tin cups and combusted using a Carlo Erba MFC 500 elemental analyser for determination of organic carbon in the sample. The $^{13}C/^{12}C$ ratios of the CO_2 was then measured with a HRGC 5300 Megaseries mass spectrometer. The $\delta^{13}C$ values were defined as:

$$\delta^{13}C\ (‰) = \frac{(^{13}C/^{12}C_{sample}) - (^{13}C/^{12}C_{standard})}{(^{13}C/^{12}C_{standard})} \times 1000$$

where the $^{13}C/^{12}C_{standard}$ refers to the value from a limestone standard ($CaCO_3$, PDB).

3.9. Estimation of thallus specific carbon (TSC) and energy equivalents in **Ascoseira mirabilis**

The thallus specific carbon content in the samples (TSC) is a biomass parameter strongly related to the thallus density and was calculated as a function of the sample area (1.5 cm diameter) and the total organic C content relative to moles (Markager & Sand-Jensen 1992, 1996). The energy equivalents were calculated

from organic C contents in the sample (g C g^{-1} DW) using the equation described by Platt & Irwin (1973):

$$E = [-0.555 + 0.113\ c + 0.054\ n]\ J$$

Where E is the energy expressed in Joules, c is the organic carbon content expressed in % DW, n refers to the nitrogen correction and J is the conversion factor from calories to Joules.

3.10. Determination of major organic constituents

Total proteins were determined colorimetrically after Bradford (1976). Samples between 30-50 mg dry weight were finely ground and then put into 10 ml reagent glasses cointaining 5 ml trichloroacetic acid (TCA). The samples were then hydrolized at 90 °C for 1 h and centrifuged at 4000 g for 15 m. The precipitate was rediluted with 1 ml 1N NaOH and after some min neutralized with identical volume of 1N HCl. To aliquots (0.1 ml) of this solution, 1 ml of protein reagent (Coomassie Brilliant Blue G-250) was added and the tubes vigorously shaked. The extinction at 595 nm was measured against a reagent blank in a spectrophotometer (Spectronic 401, Milton Roy). The protein content finally was determined using calibration curves obtained using a bovine serum albumin standard.

Total amino acids were measured spectrophotometrically according to the methodology described by Moore & Stein (1954). Algal material between 10 and 20 mg was diluted in 5 or 10 ml double destilled water, respectively. Aliquots (100 µl) were then taken and added to a solution containing 100 ml of sodium-acetate buffer (pH 5.5) and 200 ml of the amino acid reagent prepared by adding 2 g ninhydrin and 300 mg hydrindantin in the presence of ethylen glycol monomethyl ether. This solution was then incubated at 100 °C for 15 min in the dark. After dilution with 3 ml ethanol (50%), the extinction was measured at 570 nm in a spectrophotometer (Spectronic 401, Milton Roy). The amino acids were then estimated agains curves of a commercial L-Leucine standard.

Mannitol was determined by high performance liquid chromatography (HPLC) after Karsten et al. (1991). Approx 10 mg powdered material was extracted using ethanol (70 %) at 80 °C for 2 h. After centrifugation at 4000 g for 15 min, 700 ml of homogenate were dried under vacuum (Speed Vac Concentrator SVC 100H, Bachofer GmbH) overnight and re-suspended in 2 ml double destilled water. The samples were analysed in a HPLC fitted with a refractometer (Bio Rad Inc.) and two separation columns: a stainless-steel Fast Carbohydrate (Bio Rad Inc.) main column (100 x 7.8 I.D) and a Carbo-P Micro-Guard (Bio Rad Inc.) cation guard column. Double destilled water was used as eluent at a flow rate of 1 ml min^{-1} at 60 °C. Mannitol was then quantified by comparison of the retention times and peak eights with a standard solution (3.3 mM) using a chromatographic integrator (Hewlett Packard HP 3396 A).

Laminaran (ß-D-Glucopyranose) was determined in 10-20 mg dry material using 1 ml ethanol (20 %) at 75 °C for 2-3 h. After centrifugation, 0.5 ml from the supernatant was diluted in 1 ml 1N HCl and hydrolized for 1 h at 100 °C. The homogenates were then neutralized by addition of 1 ml 1N NaOH. Subsamples of 40 µl were incubated with amyloglucosidase (Boehringer, Mannheim) in citrate buffer (pH 4.6) at 55 °C for 45 min. The extracts were then diluted with 350 µl tri-ethanolamine (pH 7.6), 35 µl ATP, 35 µl NADP and 440 µl double destilled water. The extinction (Ext_1) was measured spectrophotometrically (Spectronic 401, Milton Roy) at a wavelength of 340 nm. Finally, 10 µl of a cocktail containing the enzymes hexokinase and glucose-6-P-dehydrogenase (Boehringer, Mannheim) was added and after incubation at ambient temperature for 15 min, the absorbance was read a second time at 340 nm (Ext_2). The laminaran content in the extract was then calculated using the following equation:

$$(Ext_2 - Ext_1)\ 3.22 = \text{Laminaran (mg ml}^{-1})$$

The accuracy of the method was evaluated by determining the recovery from standard solutions of commercial laminaran from *Laminaria hyperborea*.

4. MORPHO-FUNCTIONAL RELATIONS IN *ASCOSEIRA MIRABILIS*

4.1. Morphological characteristics and blade development

A very striking characteristic of several Antarctic brown algae is their morphological complexity. In the particular case of *Ascoseira mirabilis*, the large size and advanced structural organization of the perennial thallus resemble *Laminaria* species from the northern Hemisphere. Like many *Laminaria* species, *Ascoseira* possesses a strap-like lamina with an intercalary basally located meristem forming new tissue during each growth phase. Thus, the blade in this species is formed by tissues differing in age and developmental stage (Gómez et al. 1995a). On the other hand, histological studies have revealed the presence of so-called "conducting channels", which are longitudinally arranged in the medulla (Clayton & Ashburner 1990) and can be compared anatomically with the trumpet cells found in Laminariales, the "trumpet hyphae" of the Desmarestiales or the solenocysts described in the Phyllariaceae (Buggeln 1983, Schmitz 1981). Up to now, however, no conclusive evidence for a possible transport function of the conducting channels in *A. mirabilis* is available. Whereas in mature "conducting channels", the presence of dense accumulations of physodes challenges a functional role, young "conducting channels" are metabolically active and contain relatively few physodes. Moreover, the ocurrence of pit connections connecting young channels with medullary filaments add new evidence for a possible translocation function of the conducting channels, at the least in young plants (Clayton & Ashburner 1990).

The biomass allocation within the thallus in *Ascoseira* is basically determined by the timing of the meristem activity . Punched-hole experiments indicate that during the first year the blade is elongated longitudinally (Gómez et al. 1995a). In the second year, due to the activity of the basal meristem major changes in the blade shape become obvious. Tissue formation from the meristem is bi-directionally oriented and increases in width are evident (**Fig. 2**). After two

months, the basal blade region increases in width three fold, but the total length does not change much. After five months, the total length of the plant has increased by only 10 %, whereas the basal blade region is 500 % wider. The tissues formed in the last season, by contrast, do not suffer marked changes: the surface-area in the middle and apical blade region only increases by 5 % at the end of the experiment. In the third year (second growth season), the basal region becomes wavy and the first signals of senescence (deterioration and erosion) of the oldest thallus

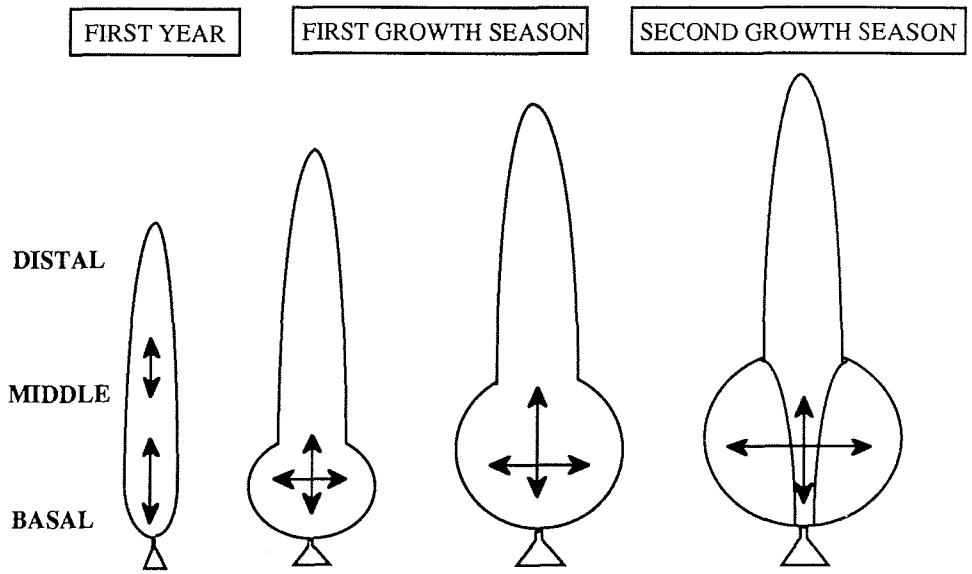

Fig 2. Development of the blade and patterns of biomass allocation in *Ascoseira mirabilis*. Arrows indicate the main growth axis along the thallus.

parts in the distal region become evident. It must be emphazised that this type of experiment refers to the dynamics of biomass allocation under culture conditions. Further processes leading to digitation of the lamina and the allometric relations in the large (up to 2 m large) *Ascoseira* plants from the field can not be examined in he laboratory. To answer these questions, further observations on morphogenesis and growth under natural conditions are needed.

4.2. Photosynthetic performance of different thallus parts along the blade

The gradients in tissue composition in *Ascoseira* involve also differentiation at the metabolic level. This hypothesis was tested in three studies on photosynthesis and related parameters in different blade regions (Gómez et al. 1995a,b, 1996). During the growth phase of culture plants in spring, net photosynthetic rates (net P_{max}) on a fresh weight basis are slightly higher in the middle region compared to the rates measured in the basal and distal regions (Gómez et al. 1995a, **Fig. 3**).

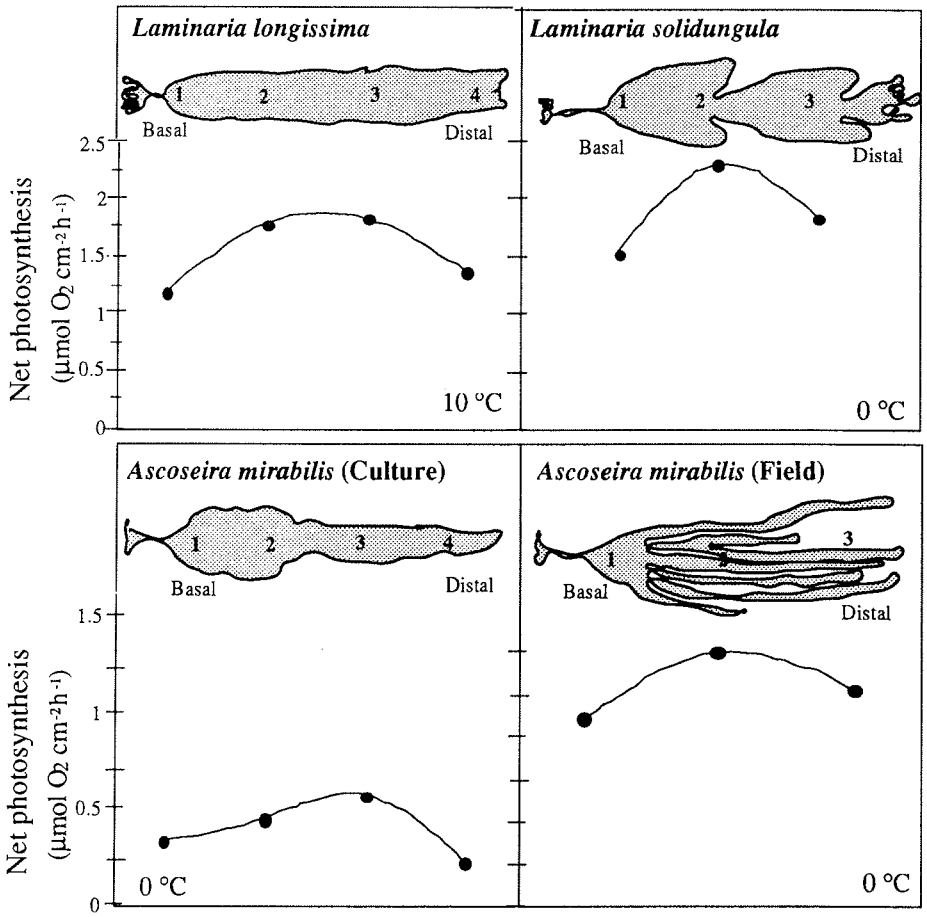

Fig. 3. Comparative longitudinal profiles of O_2-based net photosynthesis (area basis) in species of *Laminaria* and *Ascoseira mirabilis*. Data for *Laminaria longissima* and *L. solidungula* were taken from Sakanishi et al. (1991) and Dunton & Jodwalis (1988), respectively and *Ascoseira* data from Gómez et al. (1995a,b).

In field plants measured in September, this differentiation was more marked with basal regions having significantly lower net P_{max} rates (12 μmol O_2 g^{-1} FW h^{-1}) than middle and distal tissues (22-25 μmol O_2 g^{-1} FW h^{-1}; .

Longitudinal profiles of photosynthetic performance have been previously reported in some kelps eg. in the Arctic *Laminaria solidungula* (Dunton & Jodwalis 1988) and the cold-temperate *L. longissima* (Sakanishi et al. 1991). Comparatively, the species of *Laminaria* show higher net photosynthetic rates on an area basis than *Ascoseira*, however, the intra-thallus profiles are similar with the highest values occurring in the middle regions of the blade. This pattern may be directly related to the age of tissues within the blade. i. e., photosynthetic activity increases with age of the tissues reaching a maximum but then decreases with further aging. Interestingly, a considerable decrease in the distal photosynthesis was observed in those plants suffering apical erosion or senescence processes, particularly in *Laminaria* and cultured *Ascoseira*. In field plants of *Ascoseira*, no signs of tissue deterioration were detected. It is suggested that losses of senescent blade portions of field plants caused by water motion may be the reason of this situation, whereas in culture plants senescent tissues remain attached for a long time to the younger thallus parts (Gómez et al. 1995b). It must be emphazised that this longitudinal pattern of biomass allocation can be only found in species with a basally located meristem as in *Ascoseira* or *Laminaria*. In contrast, species of *Fucus* or *Sargassum* exhibiting apical growth and allocation of the oldest tissues in the basis, show the highest photosynthetic capacities in the young apical regions (Küppers & Kremer 1978, Gao & Umezaki 1988, Gao 1991). Due to these morpho-functional characteristics, the removal of apical tissues e.g., in *Fucus*, has considerably greater implications for primary productivity of this plant than e.g. in *Ascoseira*.

As mentioned above, the blade in *Ascoseira* becomes more complex with time as new tissue is incorporated to the system each growth season. Thus, two age-components must be considered: the age of the different blade tissues and the age of the whole plant. Age does not only modify the longitudinal photosynthetic

gradients but substantially affects the photosynthetic capacity and efficiency. In this context, two-year old plants of *Ascoseira* have, on a fresh weight basis, net P_{max} and α-values almost two times higher than three-year old individuals. However, other parameters such as dark respiration, saturation (I_k) and compensation (I_c) points and dry matter do not show obvious differences (Gómez et al. 1996). The photosynthetic variability accounted by the tissue age may also be seen in terms development of the photosynthetic apparatus with ontogeny. In both classes of age, middle regions have the higher net P_{max} than basal and distal regions, suggesting that photosynthesis is low due to the presence of a non-developed photosynthetic apparatus in the basal region and decreases in the oldest distal tissues due to senescence processes. The low levels of Chl *a* in these tissues may support this idea.

4.3. Longitudinal profiles of carbon-fixation

Photosynthetic C-fixation rates in highly differentiated brown algae show a similar intrinsic variation as O_2 production. Küppers & Kremer (1978) associated the increased ^{14}C-assmilation in the distal regions of *Laminaria* species with a higher activity of the Calvin cycle enzyme ribulose 1,5- bis-phosphate carboxylase-oxygenase (RUBISCO). Moreover, these authors demonstrated longitudinal profiles in light independent C-fixation in these species coupled to a high activity of the enzyme phosphoenolpyruvate carboxykinase (PEP-CK) in the growing regions (ß-carboxylation). The activities of these carboxylating enzymes respond, apparently, to the growth characteristics of *Laminaria*. In fact, *Laminaria* species from cold-temperate and Arctic regions grow in winter or under limited light conditions which could prompt the development of an alternative carboxylating mechanism (Küppers & Kremer 1978). ß-carboxylation measured as activity of PEP-CK is also linked to the growth requirements of these plants. For example, light-independent carbon fixation provides C-skeletons (preferentially amino-acids) for both biosynthesis and anabolic processes thus compensating, partially, for C losses due to respiration during active growth.

Particularly, in the meristematic region of *Laminaria*, PEP-CK uses CO_2 lost in glycolysis of mannitol translocated from the distal region to the meristem (Kremer 1981, Kerby & Evans 1983). In *L. hyperborea*, light-independent carbon fixation can account for more than 30 % of the total total light C-fixation in the growing region (Kremer 1981).

The patterns of C-fixation obtained in *Ascoseira* exhibit also intra-blade variations (Gómez et al. 1996), however, some differences with respect to patterns measured in *Laminaria* are observed (**Fig. 4**). On the basis of profiles measured using eight sampling zones along the blade it was found that photosynthetic C-fixation increases with tissue age reaching a maximum in the middle blade. In the distal regions values remain relatively constant, supporting the statement that senescence processes in the oldest tissues affect carboxylation to a minor degree than O_2 production (Küppers & Kremer 1978). Maximum light C-assimilation rates of 75 μmol C g^{-1} DW h^{-1} *Laminaria digitata* and *L. saccharina*, respectively, are higher than those measured in *Laminaria hyperborea* (21 μmol C g^{-1} DW h^{-1}) and *Ascoseira mirabilis* (45 μmol C g^{-1} DW h^{-1}).Light-independent C-fixation rates in *Ascoseira* were, in contrast to *Laminaria* species, substantially higher increasing towards the distal oldest regions of the blade (maxima close to 26 μmol C g^{-1} DW h^{-1}).

In general, dark C-fixation represents between 24 % (Gómez et al. 1995a) and 65 % (Gómez et al. 1996) of light C-fixation in the distal blade region in *Ascoseira*. These values are comparable to ratios found in species of *Laminaria*. Growing regions of *L. digitata* and *L. saccharina* exhibit maximum light independent C-fixation rates close to 8 and 4 μmol C g^{-1} DW h^{-1}, respectively, which is close to 21 % of photosynthetic C-assimilation. Such proportions, however, can increase up to 67 % in the basal blade tissues of *L. hyperborea*. The different thallus allocation of dark C-fixation in *Ascoseira* may be related to the high dark respiration rates observed in distal blade regions as C fixed in the dark was 46 % compared to dark respiration (Gómez et al. 1995a, 1996). It is not clear, however, whether light independent C-fixation may compensate for C

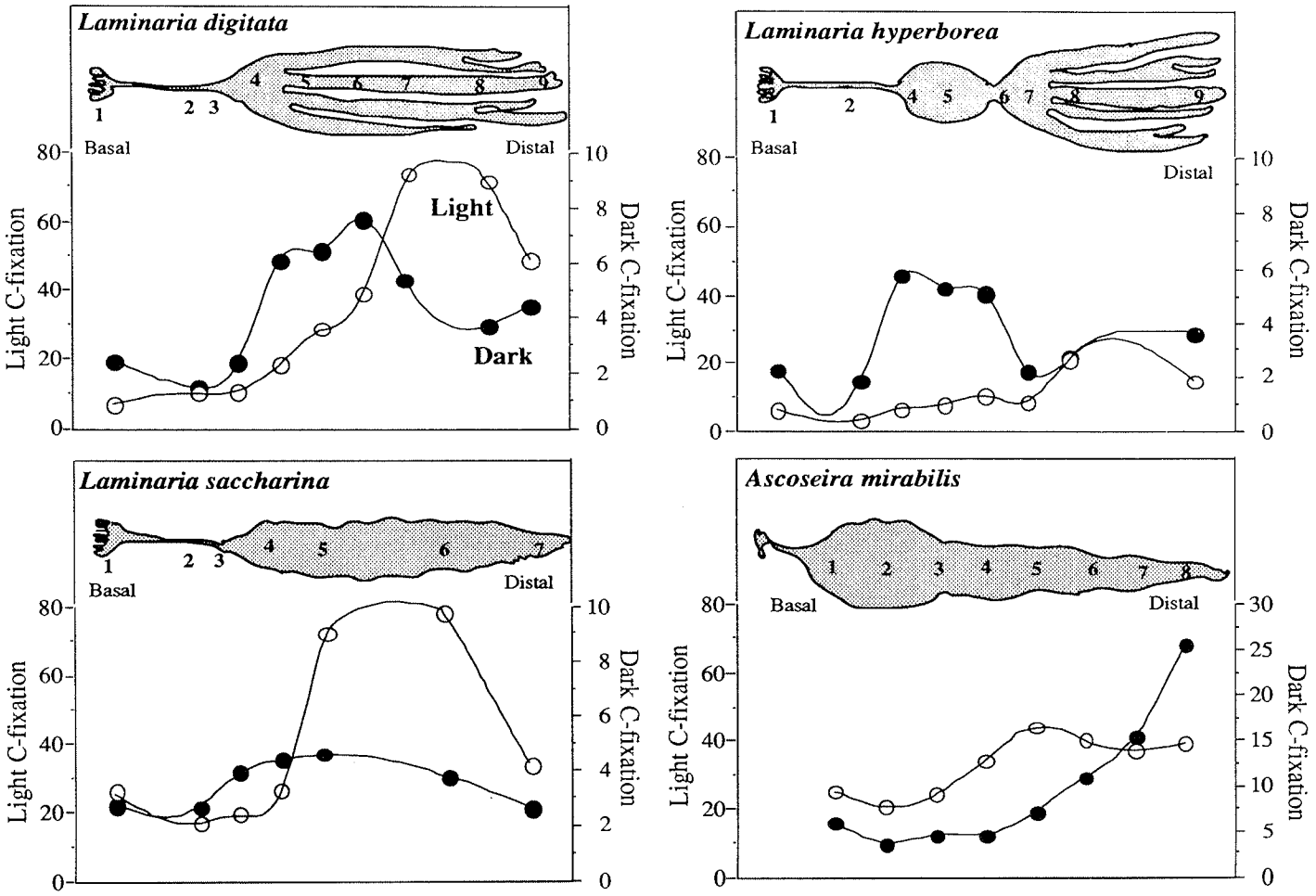

Fig. 4. Comparisons of intra-thallus variation in light and dark ^{14}C-fixation in species of *Laminaria* and *Ascoseira mirabilis*. Data were redrawn from Küppers & Kremer (1978) and Gómez et al. 1995a. Open circles: light C-fixation, closed circles: dark C- fixation

losses due to respiration as pointed by Kremer (1981). In a previous study, Thomas & Wiencke (1991) did not conclusively demonstrate a relationship between light independent C-fixation and dark respiration in several Antarctic marine algae. In general, dark C-fixation was between 4.9 and 31 % of dark respiration in five brown algae and one Rhodophyte. In species such as *Himantothallus* and *Desmarestia anceps* low dark C-assimilation rates were coupled to high respiration rates. This situation was also found in *Ascophyllum nodosum* indicating that in the dark there was always a net C loss due to respiration (Johnston & Raven 1986). It must be kept in mind that estimations of photosynthesis (or dark respiration) using O_2 based techniques are generally not comparable to those using ^{14}C-fixation measurements as ^{14}C techniques do not measure C losses via respiration (Andersen & Sand-Jensen 1980, Williams 1993). Thus, only apparent photosynthetic quotients (O_2 produced:C assimilated; PQ) can be calculated which do not always describe accurately photosynthesis in marine organisms (Laws 1991). Despite all these considerations, the findings that O_2-based photosynthesis and ^{14}C-fixation vary as a function of blade development in *Ascoseira* add new evidence to a convergent morpho-functional evolution of this species with respect to large Laminariales. In this case not only morphological organization but also a metabolic differentiation along the blade constitute common characteristics of both taxa.

5. HETEROMORPHIC LIFE HISTORY AND PHOTOSYNTHESIS IN *DESMARESTIA MENZIESII*

5.1. Life-history characteristics in brown algae

Heteromorphic life history in macroalgae has drawn the attention of a lot of phycologists during the last decades. The ecological and evolutionary implications of the alternation of generations in brown algae were discussed by Clayton (1988). This author indicates that the acquisition of perennial characteristics in the macrothallic sporophytic generation particularly of the highly advanced taxa leads to a reduction of the microthallic gametophytes. The ultimate step in this evolutionary trend is observed in members of the Fucales and Ascoseirales, which lack free-living gametophytes. In Laminariales and Desmarestiales, free-living gametophytes are still present, however, they are morphologically inconspicuous, generally constituted of microscopic filaments and only important in sexual reproduction. In contrast, large sporophytes attain complex anatomical characteristics, they are generally perennial and have a greater reproductive capacity than gametophytes being thus better adapted to withstand the physical and biological environment. However, the ecological factors and mechanisms involved in such a morphological expression are, up to date, not clear and in many cases, contradictory interpretations about its selective significance have been proposed. Neushul (1972) suggested that the dissimilar reproductive phase expression in large kelps may be primarily associated with a differential response to wave action. Later, diverse studies assigned herbivory as the main factor determining heteromorphic phase expression in algae with crustose and upright thalli (Slocum 1980, Lubchenco & Cubit 1980, Dethier 1981). Physical factors were also regarded as the ecological determinants. For example in the small brown alga *Scytosiphon lomentaria*, a postrate crust alternates with the erect fronds to withstand sand burial or persist as an over-wintering (Littler & Littler 1983) or over-summering stage (Clayton 1988). Culture studies on several brown algae added further evidence that the expression and viability of a morphological

component within the life-history may also be governed by environmental factors such as daylength, irradiance levels and temperature (Kain 1964, 1965, Lüning & Neushul 1978, Lüning 1980, Fain & Murray 1982, Novaczek 1984, Dieck 1993). In the particular case of the Desmarestiales, evidence indicates that reproduction and further development of gametophytes and sporophytes are regulated by an interaction between temperature and photoperiod. For example, *Desmarestia firma* from South Africa shows development of gametophytes under short photoperiod (8 light:16 h dark) and average temperatures 3 °C higher than those required for optimum growth of sporophytes (Anderson & Bolton 1989).

5.2. Light availability and life history in Antarctic Desmarestiales

Culture studies on all members of the Antarctic Desmarestiales indicate that life history is depending strongly on seasonal daylengths. In general, the development

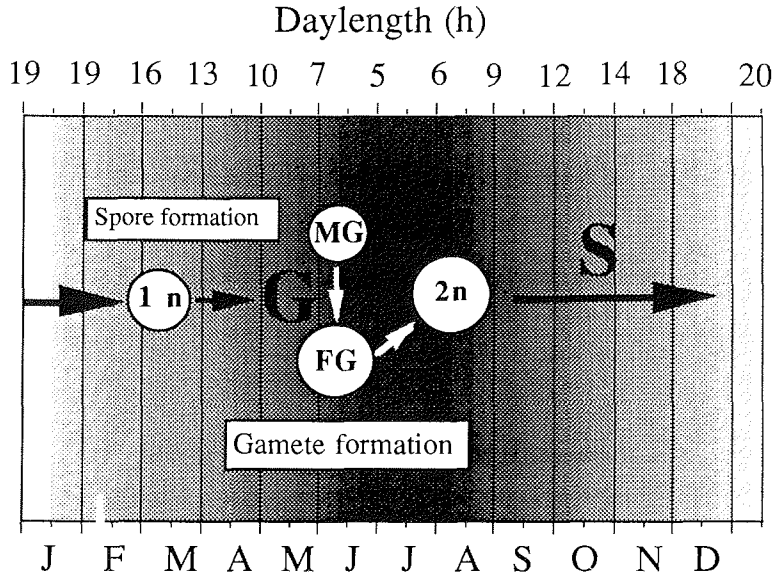

Fig. 5. Schematic diagramm illustrating the seasonal ocurrence of major reproductive events in Antarctic Desmarestiales. G: gametophytic phase; S: sporophytic phase; MG: male gametangia; FG: female gametangia. The scheme was constructed from data reported by Clayton & Wiencke 1990, Wiencke & Clayton 1990, Wiencke et al. 1991, 1995, 1996.

of gametangia, fertilization (oogamy) and early stages of sporophytes take place in winter under short daylengths in *Himantothallus grandifolius, Phaeurus*

antarcticus, and *Desmarestia* spp (**Fig. 5**), whereas growth of sporophytes begins with increasing daylengths in late winter spring. In *Desmarestia menziesii*, the entire reproduction process including gametogenesis up to early sporophytes, occurs under daylengths shorter than 9 h^{-1} in culture conditions. Irradiance levels $\leq$ 5 µmol photons m^{-2} s^{-1} are necessary to induce gametogenesis and fertilization, whereas large sporophytes require
(Wiencke et al. 1995). Apparently photon fluence rates of 10 to 13 µmol m^{-2} s^{-1} constitute the upper irradiance levels at which gametogenesis takes place in Antarctic Desmarestiales as demonstrated in *Himantothallus grandifolius* (Wiencke & Clayton 1990) and *Desmarestia anceps* (Wiencke et al. 1996). Interestingly, all of the Antarctic Desmarestiales studied up to now show *in situ* fertilization (Wiencke et al. 1995, 1996), adding new evidence on the importance of the gametophytic generation on the early stages of the large sporophyte. In terms of ecological significance, the recruitment of sporophytes and consequently the observed dominance of these species would be conditioned by the survival (or mortality) of female gametophytes. Unfortunately, such an hypothesis is difficult to test in the field due to the small size of gametophytes and to the harsh environmental conditions in the Antarctic. However, as mentioned above, the development of gametophytes or at the least their reproductive capacity appears to be constrained at high light conditions suggesting that adaptiveness of the winter development of gametophytes lies partly in a differentiation in light requirements for photosynthesis.

5.3. Differential photosynthetic performance of gametophytes and sporophytes of Desmarestia menziesii

Gametophytes and small, uncorticated sporophytes show significantly higher gross photosynthetic rates in short days (7:17 L:D) than adult sporophytes, in particular, when data are expressed on a dry weight basis (**Fig. 6**). However, on a weight basis, photosynthetic performance (net P_{max}) of adult sporophytes grown in long days (16:8 h L:D, October conditions) is comparable to rates measured in

uncorticated sporophytes growing at shorter daylengths (20 *vs* 23 μmol O_2 g^{-1} FW h^{-1}). This situation demonstrates that seasonality in the daylength regimes plays an important role in the photosynthetic metabolism of sporophytes (see below) and emphazises that gametophytes and early stages of sporophytes are photosynthetically more active than adult plants, at the least under short daylength conditions. Data on photosynthetic performance of gametophytes grown under longer daylengths are not available so far for any of the Antarctic algae and thus is not possible to infer comparative advantages of this generation in spring-summer conditions.

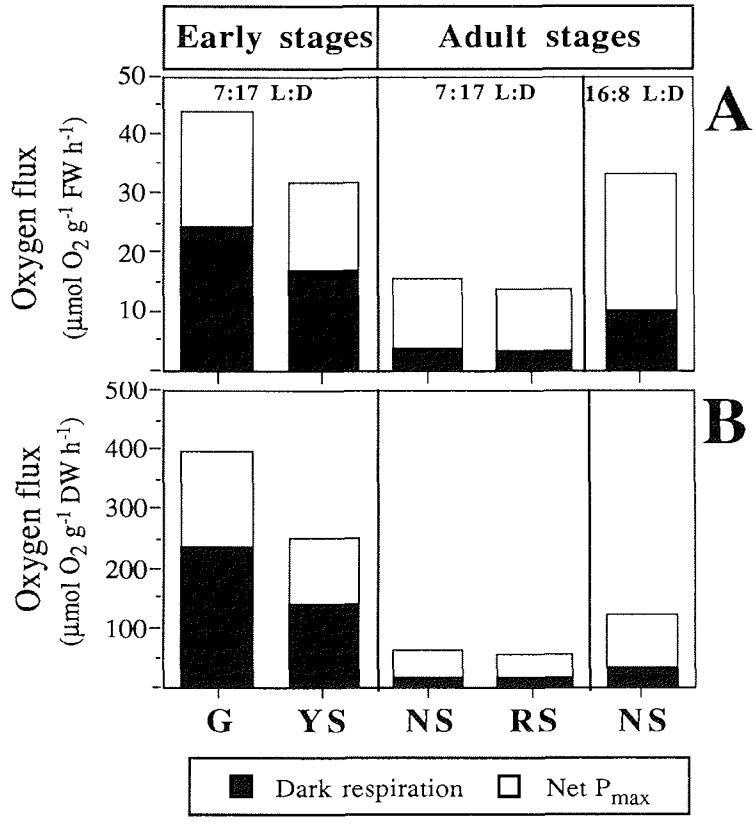

Fig. 6. Comparative dark respiration and photosynthetic (net P_{max}) rates of gametophytes and different developmental stages of sporophytes of *Desmarestia menziesii*. Oxygen evolution is expressed on a A) fresh weight and B) dry weight basis. The daylengths for growth at the time of the measurements are also indicated. Abreviations: G: gametophytes; YS: young sporophytes; NS: non-reproductive adult sporophytes; RS: reproductive adult sporophytes. Data re-drawn from Gómez & Wiencke 1996, 1997a.

Dark respiration rates were very high in gametophytes and young sporophytes indicating an increased metabolic activity. In contrast, adult sporophytes are characterized by a low respiratory activity relative to net P_{max}. The high dark respiration rates of the uncorticated sporophytes may be explained by the high growth activity as plants were measured in August under daylengths of 7:17 L:D. During this period major morphogenetic processes i. e. increase of size and number of cells, formation of the cortex formation of intercalary meristems in primary laterals take place (Wiencke et al. 1995). Such processes imply high energy costs which may be supplied via anabolism. Interestingly, the high respiration rates in gametophytes may not be related to biomass formation processes because these plants have a limited growth. Instead, reproductive processes rather than growth may explain the high respiration rates. The fact that a relatively important fraction of the cellular mass in the dioecious gametophytes during reproductive periods is constituted by oogonia or spermangia (Wiencke et al. 1995) may support this idea. In contrast, the low relative proportion of reproductive tissues to the total cell mass in adult reproductive sporophytes may account by the scarse effect of reproduction on the net P_{max} and dark respiration in these plants.

Results from temperate species indicate that net P_{max} and dark respiration among different morphotypes (not necessarily distinct generations) are generally different (**Table 4**). In general, photosynthesis measured in adult sporophytes does not exceed 33 % of the photosynthetic rates achieved by gametophytes. In the brown algae *Macrocystis pyrifera*, showing a comparable heteromorphic expression as *Desmarestia menziesii*, photosynthesis of large sporophytes relative to gametophytes varies between 14 and 33 %. Moreover, in both species, net P_{max} measured in adult sporophytes represents 50% of that measured in young sporophytes. This ratio decreases in *Desmarestia antarctica*, with adult sporophytes having only 15% of the photosynthesis of

Table 4. Photosynthetic performance of adult sporophytes relative to gametophytes and young sporophytes in different species of macroalgae. P_G: net P_{max} gametophytes; P_{AS}: adult sporophytes; P_{YS}: young sporophytes. Values correspond to % ratios.

Species	P_{AS}/P_G (%)	P_{AS}/P_{YS}	Reference
Macrocystis pyrifera [a]	14-33	50	Fain & Murray (1982)
Scytosiphon lomentaria [b]	6.2		Littler & Littler (1983)
Mastocarpus papillatus [c]	28.6		Zupan & West (1990)
Mastocarpus stellatus [d]	15.6		Dudgeon et al. (1995)
Desmarestia antarctica [a]		15.0	Thomas & Wiencke (1991)
Desmarestia menziesii [a]	31.9	46.9	Gómez & Wiencke 1996

[a] (mg O_2 g^{-1} DW h^{-1}) [c] (mmol O_2 mg^{-1} Chl *a* h^{-1})
[b] (mg C g^{-1} DW h^{-1}) [d] (µmol O_2 cm^{-2} h^{-1})

young uncorticated plants. In algae with erect and crustose developmental stages such as the brown alga *Scytosiphon lomentaria*, and the Rhodophyte *Mastocarpus stellatus* photosynthesis in the crustose phase may reach between 6 and 29 % of that measured in gametophytes.

5.4. Light absorption characteristics and shade adaptation of gametophytes and young sporophytes

The hypothesis that gametophytes of *Desmarestia menziesii* are better suited to live under low light conditions than adult sporophytes was also tested using data on photosynthetic efficiency (α) and light requirements for saturation (I_k) and compensation (I_c) for photosynthesis. α values measured in gametophytes and juvenile stages of sporophytes (**Fig. 7**) show five times higher photosynthetic efficiency than adult sporophytes. In contrast to net P_{max}, α values of adult sporophytes growing under a daylength of 16:8 L:D was similarly low as plants grown in short days. This indicates that, comparatively, α is a parameter more strongly affected by thallus morphology than net P_{max}. The proportion between photosynthetic to non-photosynthetic tissues underlies also differences in the assimilatory pigment content per unit weight or thallus surface area which may be

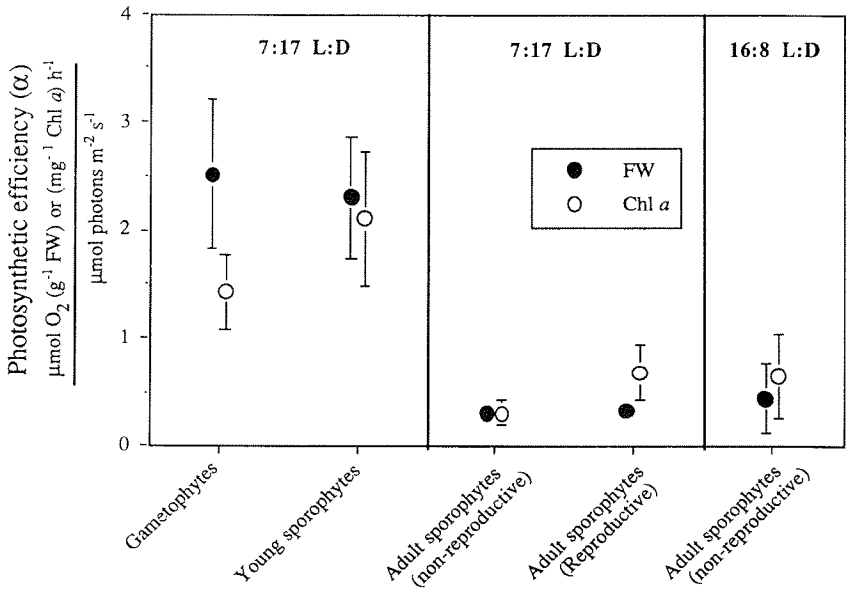

Fig. 7. Photosynthetic efficiency (a) at limiting irradiance of gametophytes and different developmental stages of sporophytes in *Desmarestia menziesii*. Oxygen production is expressed on the basis of fresh weight (FW) and Chl *a* contents. Growth daylengths at the time of the measurements are also indicated. Data are taken from Gómez & Wiencke 1996, 1997a.

directly related to the light harvesting efficiency at low irradiance (Ramus 1981). In filamentous or thin-sheet like thalli photosynthetic O_2 production as a function of pigments follows a linear curve, whereas thick morphologies, characterised by several cell layers and low photosynthetic:non-photosynthetic tissues ratios, photosynthesis becomes uncoupled of the pigment content due to a greater attenuation of the light within the thallus (Ramus 1978).

Whether differences in photosynthetic efficiency between gametophytes and sporophytes of *Desmarestia menziesii* involve also changes at the level of the photosynthetic apparatus, is not clear so far. Changes in pigment content within the thallus during the development may imply also increases in number (or size) of the photosynthetic units at a cellular level. In this sense, the lower proportion of fucoxanthin relative to Chl *a* in adult sporophytes suggests modifications in the size of the antenna reaction center with increasing thallus development (Gómez &

Wiencke 1996). It is clear, however, that light requirements for compensation of photosynthesis (I_c) are strongly determined by dark respiration and α. Because of their high respiration rates, light requirements for compensation of photosynthesis in gametophytes and small sporophytes do not significantly decrease, whereas light saturation strongly increases in adult sporophytes due to low α values. Photosynthesis of adult sporophytes saturates at significantly higher irradiances (30 µmol photons m^{-2} s^{-1}) than in gametophytes or young sporophytes ($\leq$ 16 µmol photons m^{-2} s^{-1}). Although low I_k values have been claimed to reflect an inefficient use of high irradiance rather than an efficient use of low light (Henley 1993), the results found for *Desmarestia menziesii* confirm that low I_k of gametophytes and early sporophytes may be a good indicator of shade adaptation as in cultures the irradiance was similar (10-13 µmol photons m^{-2} s^{-1}) in all the phases. On the other hand, the low I_c (5-12 µmol photons m^{-2} s^{-1}) may be related to the low irradiances required by growth of these plants. Sporophytes and gametophytes from several Antarctic Desmarestiales show light saturation of growth at irradiances close to 10 µmol photons m^{-2} s^{-1} (Wiencke 1990 a, Wiencke & Fischer 1990). According to Markager & Sand-Jensen (1992), high photosynthetic efficiencies at low light, and low respiration rates are adaptations for growth and survival of macroalgae in low light. Despite this, gametophytes and uncorticated sporophytes of *Desmarestia menziesii* exhibit very high respiratory activities. As photosynthetic compensation points normally do not agree with minimum light requirements for growth of macroalgae (Markager 1993, Markager & Sand-Jensen 1992), the results in gametophytes of the *D. menziesii* suggest that culture irradiances of 10 to 13 µmol photons m^{-2} s^{-1} are substantially higher than compensation irradiances for growth and thus plants not are constrained by high dark respiration.

Overall the evidence obtained here reveals that the ability of gametophytes and uncorticated sporophytes to grow and photosynthesize under low light conditions is adaptive. Like in the physiological differences between crustose and foliose phases in several macroalgae, which respond to the adaptive characteristics

in the life history allowing the species to survive changing environmental conditions (e.g. wave action, sand burial, dessication or herbivory), the differential photosynthetic activity of the heteromorphic phases in *D. menziesii* constitutes an adaptation that allows the algae to survive under the seasonally changing light environment. During winter, when incident irradiance is low and daylength is short, high photosynthetic rates and growth of gametophytes and uncorticated sporophytes are favoured in virtue of their fine morphology (high surface-area/volume ratio), higher pigment content and more efficient light use. In contrast, large sporophytes require greater imputs of irradiance to C assimilation and probably to compensate for tissue losses due to herbivory or ice-disturbance. The question whether heteromorphic phase expression in Antarctic Desmarestiales is also dependent on herbivory, substrate modifications or ice-action remains to be answered.

6. ANTARCTIC DAYLENGTHS AND SEASONAL PATTERNS OF GROWTH AND PHOTOSYNTHESIS

6.1. Growth

Like in the Arctic, the Antarctic region is characterized by a marked seasonality of the light conditions (Drew & Hastings 1992, Klöser et al. 1993, Kirst & Wiencke 1995). Although it was recognized that this factor directly influences the macroalgal growth, up to the begin of the nineties only few studies concerning growth and productivity were conducted. In general, much of the existing evidence that seasonal growth can effectively be triggered by changes in light conditions has been obtained using selected species, particularly large kelp-like species as *Himantothallus grandifolius*. Drew & Hastings (1992) indicated that *in situ* growth of *Himantothallus* was interrupted by ice cover to continue strongly after ice break out in spring. Interestingly, these authors reported also that some thallus regions already start to grow some weeks before the ice break out. This rose the question whether active growth of Antarctic macroalgae is simply related to light intensity or to daylength. This question was addressed using seasonally fluctuating daylengths mimicking the conditions in Antarctic. The result was that several Antarctic species grow in summer under optimum light conditions e.g. when long days and high irradiances are present ("season responder"), but also, a number of species, especially brown algae, "anticipate" the summer optimum light conditions following a seasonal pattern mainly in response to daylength (Wiencke 1990a,b). These species grow in late winter-spring similar as many members of the Laminariales from other geographic regions (Kain 1989. Lüning & tom Dieck 1989, Lüning 1990). As pointed by Klöser et al. (1993), the presence of ice cover in the Antarctic coastal systems appears to be variable in an interannual time frame distinguishing colder and warmer years (see also Clarke et al. 1988). Whether prolonged ice cover delays seasonal growth in Antarctic macroalgae is not yet clear. Recently, Weykam et al. (1997) demonstrated low growth rates in

the Antarctic red algae *Palmaria decipiens* (a season anticipator) and *Iridaea cordata* (a season responder) when exposed to darkness for several months. However, under natural conditions due to the variability of the ice cover and taking into account the extremely high water transparency of the Antarctic waters (Gieskes et al. 1987), there may be still enough light, at the least at shallow waters, making growth for macroalgae still possible (Wiencke 1990a).

Figure 8 summarizes the seasonal growth of major Antarctic brown algae grown under fluctuating Antarctic daylengths conditions. Although the algal material had different age and was grown under different culture irradiances a general pattern is clearly observed: growth on a fresh weight basis increases with increasing daylengths to reach a maximum at daylengths close to 19 and 20 h d^{-1}, while minimum growth is seen at daylengths ≤ 15 h d^{-1}. This pattern confirms

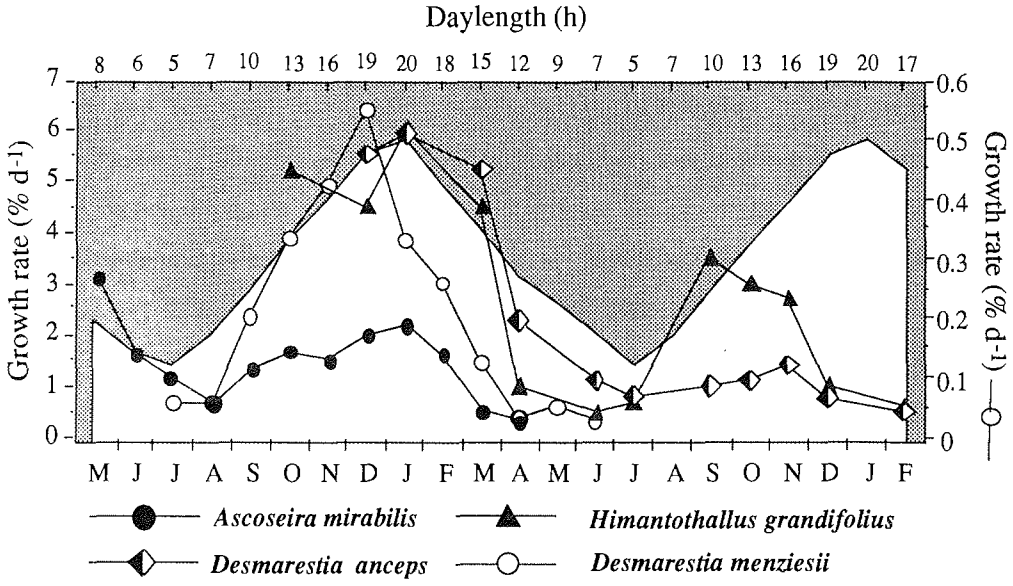

Fig. 8. Comparative seasonal growth rates of some major Antarctic brown algae cultured under simulated fluctuating daylengths. Data source: *Ascoseira mirabilis* (culture irradiance: 10-13 µmol photons m^{-2} s^{-1}, Gómez et al. 1996); *Desmarestia anceps* (7-14 µmol photons m^{-2} s^{-1}, Wiencke, umpublished); *Himantothallus grandifolius* (27 µmol photons m^{-2} s^{-1}, Wiencke 1990a); *Desmarestia menziesii* (10-13 µmol photons m^{-2} s^{-1}, Gómez & Wiencke 1997a).

that growth takes place during late winter-spring and that after a peak in early summer a rapid decrease with decreasing daylengths occurs. On the other hand, the growth peak varies in direct relation with the culture irradiance, for instance, growth peaks of *Himantothallus* grown under 27 µmol photons m^{-2} s^{-1} ocurr earlier in the season than in the other species illuminated with lower irradiances (up to 14 µmol photons m^{-2} s^{-1}). This situation might also be extrapolated to a possible effect of light attenuation due to ice-cover in the field. A prolonged ice-cover may effectively delay growth peaks but not necessarily the start of growth as in all the algae thallus elongation begins at daylengths between 5 and 7 h d^{-1} (Wiencke 1990a, b, Gómez et al. 1996, Gómez & Wiencke 1997a). It is, therefore, reasonable to assume that daylength is the major trigger for start of growth in these species (see also below).

Another factor affecting the magnitude of growth rates is thallus morphology. As mentioned above, the perennial characteristics of these species imply both ageing and an increase of biomass. Algae such as *Desmarestia* or *Ascoseira* can attain a length of up to 6 m, whereas *Himantothallus* can even reach 20 meters in length. Similarly, increasing age and size lead to a lowering in the growth activity of algae during culture. As demonstrated in *Desmarestia menziesii*, at the begin of the growth season the weight of the whole plant increases accordingly, but when growth rates decrease, weight remains constant (Gómez & Wiencke 1997a). In this context, thallus characteristics are the result of the combined action of ontogenetic changes and mass increases and can be analysed in terms of an efficient allocation of energy or as a response to biological and physical factors (Khailov et al 1978). Active growth of sporophytes in late winter-spring seems firstly to be a strategy optimizing the use the short light window between ice cover in winter, phytoplankton blooms in late spring and turbid melt water in summer which normally constrain the irradiance available for macroalgal growth (Klöser et al. 1993). On the other hand, plant growth may be restricted to late-winter spring to avoid excessive losses of new tissue due to physical detrimental factors (wave action, herbivory or ice abrasion) during other

seasonal periods. It is relatively well know that the probability of removal by physical factors increases with plant size (Santelices et al. 1980, Koehl 1986, Shaughnessy et al. 1996), therefore, a programmed seasonal growth might imply a selective advantage in the seasonally changing Antarctic environment. On the other hand, a rapid biomass formation may enhance the reproductive capacity of sporophytes in late summer or outcompete other species. In this sense, various ecological studies have documented that size and other morphological characteristics can be key elements for the dominance of a species given (Klöser et al. 1994, 1996). Additionally, evidence on selective comsumption by invertebrates and fishes shows that Antarctic macroalgae may escape from herbivory in virtue of their thallus structure, size or contents of chemical defenses (Richardson 1977, Iken 1996, Iken et al. 1997).

It has been suggested that growth patterns and other biological processes in Antarctic macroalgae may be comparable to those of macroalgal assemblages from temperate regions (Dieckmann et al. 1985, Wiencke 1990b). In general, the scarce number of *in situ* growth studies conducted in Antarctic brown algae make comparisons difficult. However, if the few data from Antarctic macroalgae are compared with data from other geographical regions (**Table 5**), it clearly emerges that growth in large macroalgae, irrespective of their habitat, follows a marked seasonality. Drew & Hastings (1992) reported that *Himantothallus grandifolius* from Signy Island (South Orkneys), elongates at rates close to 1.5 mm d^{-1} during the growth phase in spring and increases its lamina for approx. 34.5 cm within a year. These rates are comparable to seasonal maxima of lamina elongation measured in *Laminaria solidungula* from the high Arctic (Dunton 1985). On a yearly basis, the length of the lamina in *L. soligungula* increases approx. 50 cm. However, the linear daily growth rates in *Himantothallus* can become higher (6 mm d^{-1}), as reported by Dieckmann et al. (1985). Taking into account that these latter authors measured elongation during a period of low growth rates in summer, an even larger lamina elongation in *Himantothallus* on a yearly basis can be expected. The low elongation rates of *Ascoseira mirabilis*

Table 5. Comparative linear growth rates (thallus elongation) of different large brown algae measured *in situ* from different geographical regions. Values represent maxima and minima reported in each study and the corresponding estimates of yearly elongation. Values are approximate and were in some cases recalculated from diagrams showing seasonal growth rates.

Species	Location	Minimum	Maximum	Total elongation	Reference
		(mm d^{-1})		(cm)	
Cold-temperate:					
Alaria esculenta[a]	Newfondland (Canada)	0.7-1.4 (June)	4.2-5.1 (Sept)		Buggeln (1974)
Laminaria longicruris	St. Margaret`s Bay (Canada)	4 (Sept)	11.3 (June)	89 (7 months)	Hatcher et al. (1977)
	St. Margaret`s Bay (Canada)	0.35 (July-Aug)	9 (May-June)	172 (yearly)	Chapman & Craigie (1977)
Laminaria hyperborea	Berfjördur (Iceland)	1 (Oct-Nov)	8 (April-May)	107 (9 months)	Sjøtun & Gunnarsson (1995)
Laminaria spp.	Norway (West coast)	< 0.5 (Aug-Oct)	3 (April-June)	70 (yearly)	Sjøtun et al. (1996)
Lessonia nigrescens	Los Molles (central Chile)	1.5 (March-April)	2.5 (Oct-Dec)	150 (yearly)	Santelices & Ojeda (1984)
Arctic:					
Laminaria solidungula	Stefansson Sound (Alaska)	0.25 (Aug-Oct)	1.4 (Feb-April)	45 (yearly)	Dunton (1985)
	Stefansson Sound (Alaska)			15-50 (yearly)	Dunton (1990)
Laminaria saccharina	Stefansson Sound (Alaska)	0.2 (Nov-Feb)	4.5 (May-July)	83 (yearly)	Dunton (1985)
Antarctic:					
Himantothallus grandifolius	King George Island		6 (Feb-March; mean)		Dieckmann et al. (1985)
	Signy Island (South Orkneys)		1.5 (Aug-Dec; mean)	34.5 (yearly)	Drew & Hastings (1992)
Ascoseira mirabilis[b]	King George Island	0.13 (May-June)	0.5 (Aug-Sept)	6.2 (6 months)	Gómez et al. 1996

[a] Tank culture

[b] Laboratory culture (2 L volume)

(**Table 5**), which were measured under culture conditions, contrast to the growth rates on a fresh weight basis described above. As pointed out by Gómez et al. 1995b, culture plants are constrained in their growth due to the space limitation and their lamina elongation may not be representative of the actual *in situ* growth of this species. This contrasts with the situation reported for *Laminaria digitata*, indicating similar rates of lamina expansion between culture and field plants (Drew 1983). In any case, *Ascoseira* plants exhibited a clear seasonality, with elongation rates of late winter-spring being almost four times those measured in winter conditions.

Thallus elongation in cold-temperate kelps shows higher rates than in polar species. Algae such as *Laminaria longicruris* or *L. hyperborea* can grow rapidly and attain a large size in a short time (Hatcher et al. 1977, Chapman & Craigie 1977, Sjøtun & Gunnarsson 1995). However, it may be emphasized that some of the differences found among species can be accounted by the age of the plants at the time of the measurements. When plants become larger growth rates considerably decrease, a fact previously established for different kelps (North 1971, Kain 1987). This is clearly the case in *Lessonia nigrescens*, where low thallus elongation rates of established adult plants clearly contrast with the more active and relatively more constant growth of young recruited individuals (Santelices & Ojeda 1984).

Beside the light conditions, the seasonal availability of nutrients and the temperature regime are regarded as triggers of seasonal macroalgal growth (Lüning & tom Dieck 1989, Lüning 1990). The seasonal variation in nutrient concentrations was regarded as major factor determining the growth of kelps from the northern Hemisphere (Hatcher et al. 1977). Typically it was recognized that low N levels during summer limit lamina expansion and that high concentrations in winter would favour plant growth. Some species such as *Laminaria solidungula* appear to be highly adapted to cope with variations in nutrients growing almost exclusively under darkness in winter (Dunton & Schell 1986). For Antarctic macroalgae, no evidence for nutrient limitation exists. High

N contents traditionally reported for different Antarctic coastal systems (Gordon & Molinelli 1982, Clarke et al. 1988, Drew & Hastings 1992) lead to the primary conclusion that macroalgae not are nutrient limited, however, a conclusive rejection of nutrients as a regulator of macroalgal growth in the Antarctic is not possible as no studies on this topic have been performed (see below).

Although temperature is a major factor governing seasonal phenology of macroalgae from other geographic regions and is the most important environmental component affecting biogeographic distribution (see Lüning 1990), its role on the seasonality of Antarctic macroalgae has not comprehensively been established. It is known that Antarctic macroalgae are highly adapted to grow and photosynthesize at temperatures around 0 °C (Wiencke & Dieck 1989, 1990), however, no information concerning variations in growth under slight changes in temparature are available. Therefore, further studies are essential in these topics to fully understand the components of biomass formation and seasonality of Antarctic macroalgal assemblages.

6.2. Seasonal changes in photosynthesis and dark respiration

Photosynthesis is closely linked to the changes in growth as carbon assimilation supplies the necessary substrates for biomass formation. However, such a widely accepted relationship becomes complicated in polar macroalgae as frond elongation and carbon assimilation *via* photosynthesis are restricted generally to a short seasonal period, i. e., when favourable conditions of daylength or light intensity are present. As outlined above, the acquisition of an optimal size as rapid as possible appears to be a major adaptation in large species of *Laminaria* and Antarctic macroalgae and results in a synchronization of both processes e. g. thallus elongation and carbon assimilation. For example, maximum rates of growth and photosynthesis in the Arctic *Laminaria solidungula* occur in different seasonal periods: growth under darkness in winter and photosynthesis during the spring-summer open water (Dunton & Schell 1985). This pattern contrasts clearly

with the seasonal strategy observed in Arctic populations of the Arctic-cold temperate *Laminaria saccharina*, whose growth is entirely powered by photosynthesis from late-winter spring onwards (Dunton 1985, Dunton & Jodwalis 1988, Henley & Dunton 1995).

The seasonal changes in photosynthesis and dark respiration of Antarctic macroalgae are also linked to growth patterns. **Figure 9** shows the variations in net P_{max} determined in field plants of the "season anticipators" *Ascoseira mirabilis*, *Desmarestia menziesii* and *Himantothallus grandifolius*. For comparative purposes, a "season responder", *Adenocystis utricularis*, is also included. In *Himantothallus*, net P_{max} decreases between March and June (autumn), but peaks strongly in November decreasing again in December (Drew & Hastings 1992). Increased net P_{max} in November is also observed in *Desmarestia menziesii* (Gómez et al. 1997b) but not in *Ascoseira mirabilis*. In this latter species, maximum net P_{max} values are recorded in September and February (no data available between February and September; Gómez et al. 1995b). The data on *Adenocystis utricularis*, whose net P_{max} values gradually decrease from autumn onwards (Gutkowski & Maleszewski 1989), indicate no seasonality of net P_{max}, contrasting with the situation in the other species whose photosynthetic capacities increase with increasing daylength. It must, however, be emphasized that α-values in field plants of *A. utricularis* show a clear seasonal pattern with higher values in late winter-spring than in summer (Gutkowski & Maleszewski 1989).

The findings indicating high respiration rates in *Ascoseira* and *Desmarestia menziesii* during late winter-spring are the first described for Antarctic brown algae and suggest an active growth in this period (Gómez et al. 1995b,1997b). Interestingly, high respiration rates are also found in *Himantothallus*, and in some months they exceed net P_{max} (negative P/R ratio). Using models of carbon accretion, Drew & Hastings (1992), predicted more C losses in winter-early spring than C-gains, but when the annual C balance is calculated, a positive carbon

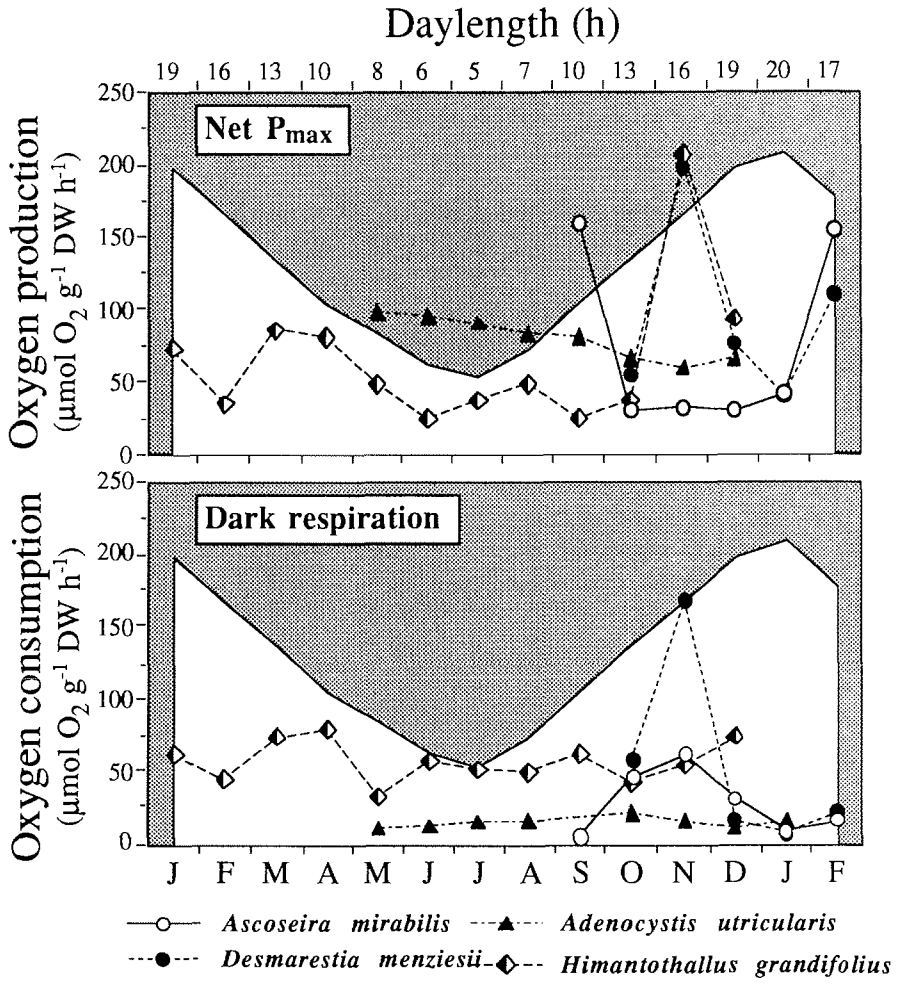

Fig. 9. Seasonal changes in photosynthesis (net P_{max}) and dark respiration, on a dry weight basis, of Antarctic macroalgae collected in King George Island and Signy Island. Data from *Adenocystis utricularis, Ascoseira mirabilis* and *Desmarestia menziesii* were taken from Gutkowski & Maleszewski (1989), Gómez et al. 1995b, 1997b, respectively and correspond to laboratory measurements (O_2 method) of field plants. *Himantothallus grandifolius* was measured in situ (^{14}C and O_2 Method; Drew & Hastings 1992).

budget can be estimated. As was outlined above, field plants need to achieve rapid thallus elongation during a short time period in late winter-spring, which implies a high respiratory activity. If respiration exceeds assimilation, then, plants necessarily utilize other mechanisms to optimize metabolic balance for support of growth. In this context, high light-independent C fixation, which accounts for a

significant fraction of the whole assimilated C (up to 65 %) in species such as *Ascoseira mirabilis* (Gómez et al. 1996) or *Desmarestia anceps* (Thomas & Wiencke 1991), may partially compensate, on a seasonal basis, for C losses.

High respiration rates exceeding net P_{max} during late-winter spring, are not only found in large field plants. In cultured macroalgae (**Fig. 10**), P/R ratios

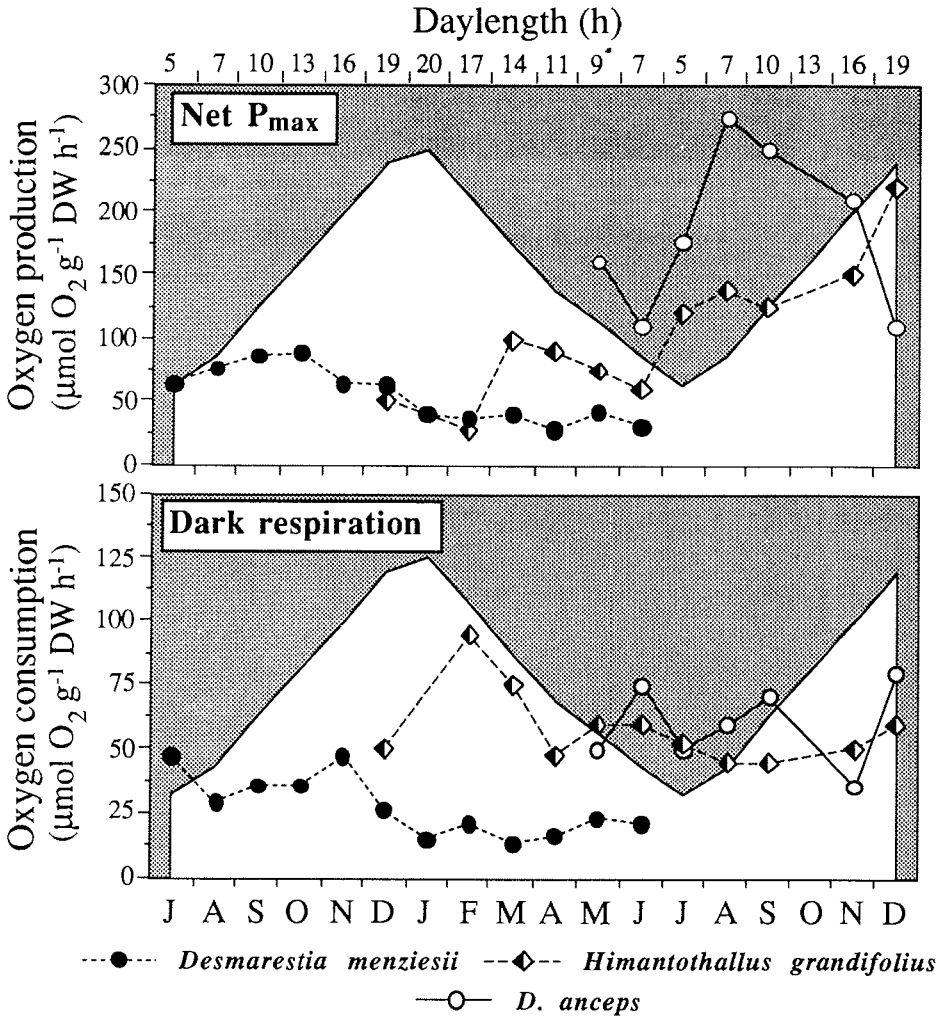

Fig. 10. Seasonal changes in O_2-based photosynthesis (net P_{max}) and dark respiration of Antarctic macroalgae cultured under simulated Antarctic daylength conditions. Data on *Desmarestia anceps* and *Himatothallus grandifolius* were taken from Daniel (1992) and *D. menziesii* from Gómez & Wiencke 1997a.

close to 1 are observed in July for *Desmarestia menziesii*, and January for *D. anceps*. In *Himantothallus*, negative P/R ratios were observed between December and June. Assuming an adequate nutrient supply, non limiting light for photosynthesis, constant temperature and absence of simulated ice-cover, then a negative C balance in the thallus is certainly the result of high growth rates. In the case of *Desmarestia menziesii*, it was clearly demonstrated that net P_{max} peaks occur earlier than peaks of dark respiration and growth which optimizes the use of photoassimilates, i. e. photosynthesis supplies the substrates for anabolism and biomass formation (Gómez & Wiencke 1997a). The direct relation between high growth rates and elevated dark respiration is observed when both species of *Desmarestia* are compared. In fact, *Desmarestia menziesii* shows significantly lower growth rates than *D. anceps*, which, however, had dark respiration rates and net P_{max} almost two times higher than *D. menziesii* (see also **Fig. 9**). Differences in plant age between both species at the moment of the measurements (2-3 year old *D. menziesii* plants *vs* 1-2 year old *D. anceps* plants; Daniels 1992) may surely account for these differences and confirm that the dark respiration as a good indicator of the metabolic status in these species. In any case, the results up to now agree in that seasonal growth is closely linked with photosynthesis and dark respiration.

6.3. Seasonal changes in photosynthetic efficiency

Wiencke et al (1993) reported for the first time data on photosynthetic efficiency of several cultured Antarctic macroalgae. The α values of *Ascoseira mirabilis* [2.4 μmol O_2 g^{-1} DW h^{-1} (μmol photons m^{-2} s^{-1})$^{-1}$], *Desmarestia anceps* [4.09 μmol O_2 g^{-1} DW h^{-1} (μmol photons m^{-2} s^{-1})$^{-1}$] and *Himantothallus grandifolius* [7.3 μmol O_2 g^{-1} FW h^{-1} (μmol photons m^{-2} s^{-1})$^{-1}$] are significantly higher when compared to α values reported for *Laminaria solidungula* (between 0.25 and 0.6 μmol O_2 g^{-1} DW h^{-1} (μmol photons m^{-2} s^{-1})$^{-1}$; Dunton & Jodwalis 1988). The findings served to characterize Antarctic algae as shade adapted organisms. In *Ascoseira mirabilis*,

high α values close to 10 μmol O_2 g^{-1} FW h^{-1} (μmol photons m^{-2} $s^{-1})^{-1}$] were found in September, but strongly decrease from October onwards to reach values close to 2 μmol O_2 g^{-1} FW h^{-1} (μmol photons m^{-2} $s^{-1})^{-1}$ (Gómez et al. 1995b). A different picture is observed in *Desmarestia menziesii*: in this species a very low α was measured in October [0.8 μmol O_2 g^{-1} FW h^{-1} (μmol photons m^{-2} $s^{-1})^{-1}$], increasing strongly in November up to 8 μmol O_2 g^{-1} FW h^{-1} (μmol photons m^{-2} $s^{-1})^{-1}$ and decreasing again towards summer (Gómez et al. 1997b). Similarly, culture plants of this species show comparable α values which peak in October and decrease during August-September and December to April (Gómez & Wiencke 1997a).

These clear seasonal changes in α values suggest adjustments in the light absorption efficiency in these algae. However, much of the data on α, do not closely correlate, on a seasonal basis, with variations in pigment contents. It has been shown that Chl *a*, Chl *c*, and fucoxanthin contents from culture material of *Desmarestia menziesii* increase as a function of the increasing thallus weight (Gómez & Wiencke 1997a). In general, it was observed that during the growth phase in late winter-spring, pigment contents can increase, but this is not a common characteristic as demonstrated by the weak correlations in other Antarctic brown algae (**Table 6**). The difficulty of relating Chl *a* to photosynthetic efficiency in several large brown algae are complicated by the fact that Chl *a* often increases still after onset of growth. As a result, mature and senescent blade tissues of *Macrocystis pyrifera* can have higher Chl *a* contents than immature or young tissues (Wheeler 1980, Arnold & Manley 1985). Similarly, Henley & Dunton (1995) concluded that the accumulation of pigments with size in *Laminaria solidungula* and *L. saccharina* is better explained by developmental processes than by photoacclimation. It may be that Chl *a* increases to compensate the increase in non photosynthetic tissues with age. On the other hand, photosynthetic efficiency in leathery and terete macroalgae are not directly correlated to pigments contents due to their high proportion of non-

Table 6. Relationship between Chl *a* content and photosynthetic efficiency (α) on a weight basis of different Antarctic macroalgae. Equations are the most accurate function describing the relation. Asterisk indicates $p< 0.05$.

Species (Season)	Equation	r^2	Data source
Ascoseira mirabilis (September-February; Field)	$Y= 0.83 X - 1.31$	0.13	Gómez et al. 1995b
Desmarestia menziesii (October-February; Field)	$Y= 0.04\ 10^{0.3 X}$	0.80	Gómez et al. 1997b
Desmarestia menziesii (July-December; Culture)	$Y= 0.63 X + 0.45$	0.83*	Gómez & Wiencke 1997a
Desmarestia anceps (July-December; Culture)	$Y= 0.93 X + 1.15$	0.26	Daniel (1992)

photosynthetic tissues (Ramus 1978). Thus, algae show seasonal fluctuating *a* values (photoacclimation), whereas their pigment contents increase almost independently on the season up to the final plant size is achieved (Gómez & Wiencke 1997a).

6.4. Seasonal changes in photosynthetic light requirements

High photosynthetic efficiencies generally determine low saturation (I_k) and compensation (I_c) points of photosynthesis. As Antarctic macroalgae are exposed for a large part of the year to very low irradiances, light requirements for photosynthesis, are also very low. I_k values reported in field plants of *Ascoseira mirabilis* during September-February increase from 20 µmol photons m^{-2} s^{-1} to 50-60 µmol photons m^{-2} s^{-1}, whereas in *Desmarestia menziesii* values may vary between 25 and 100 µmol photons m^{-2} s^{-1} in the same period. It must, however, be emphasized that these maximum saturation irradiances are substantially higher than irradiances required for saturation of growth in Antarctic macroalgae (generally $\leq$ 15 µmol photons m^{-2} s^{-1}; Wiencke & Fischer 1990, Wiencke 1990a,b), which has been established also in temperate species (Ramus et al. 1976a, Markager & Sand-Jensen 1992). Apparently, photosynthetic I_k values

above the light requirements for growth results in ecological advantages to cope with the strong fluctuations of the incident irradiance during the period of open-water in several Antarctic shallow waters (Klöser et al. 1993, Gómez et al. 1997a). In spring, when high water transparencies and increasing daylengths (light window; see above) are present, macroalgae growing at depths below 20 m can still be exposed to irradiances ≥ 80 µmol photons m^{-2}. Under these conditions, net production is less constrained by high dark respiration rates and because the number of hours for which algae are exposed to irradiances above saturation (H_{sat}) are longer, a positive net metabolic C balance may be expected (Gómez et al. 1997a, discussed below). On the other hand, when incident irradiances decrease, light requirements for photosynthesis of the algae may also decrease in virtue of their high α values. Interestingly, the hypothesis of a possible acclimation potential of plants at the prevailing light conditions, i. e. modifications of I_k, up to now has been not tested. In general, diverse culture studies reveal that such an acclimation in Antarctic macroalgae is unlikely as algae cultivated by long periods at constant irradiances of 10 to 15 µmol photons m^{-2} have I_k always above these ranges (**Table 7**). When algae are cultivated at higher irradiances (25-55 µmol photons m^{-2}) no obvious increases in I_k are observed. Only in *Ascoseira mirabilis*, a clear increase of I_k with increasing culture irradiance could be demonstrated (Wiencke et al. 1993). In other species such as *Desmarestia menziesii* or *Himantothallus grandifolius*, there are marked differences in I_k values between plants cultivated under similar light conditions. On the basis of these results, it may be argued that I_k is an unpredictable photosynthetic component and it may not be a good indicator of seasonal photoacclimation of sporophytes. Instead, changes in I_k seem to be useful, for example,when gametophytes and adult sporophytes are compared (Gómez & Wiencke 1996). Because of their small size, gametophytes and small sporophytes have, perhaps necessarily, developed adaptations to photosynthesize and grow under very restricted ranges of irradiance, which are determined by limited light

Table 7. Light requirements for photosynthesis of cultured Antarctic brown algae in relations to the growth irradiance.

Species	Culture irradiance	I_k	Reference
	(µmol photons m^{-2} s^{-1})		
Himantothallus grandifolius	10	26.3 (7.6)	Daniels (1992)[a]
	25-55	18.6 (3.5)	Wiencke et al. (1993)
	7-12	15.5 (1.5)	Melchersmann (1996)
Desmarestia anceps	10	34.7 (10.5)	Daniels (1992)[a]
	25-55	32.3 (1.8)	Wiencke et al. (1993)
	7-12	49.1 (13.0)	Melchersmann (1996)
Desmarestia menziesii	13	21.7 (4.9)	Gómez & Wiencke 1997a[a]
	10-13	53.6 (19.4)	Gómez & Wiencke 1996
Ascoseira mirabilis	25-55	40.3 (5.5)	Wiencke et al. (1993)
	10-13	19.1 (3.6)	Gómez et al. 1996
	7-12	15.6 (2.9)	Melchersmann (1996)
	10-13	14.0 (2.5)	Gómez et al. 1995a

[a] annual average

conditions in winter, the canopy effect of adult sporophytes or the presence of ice cover. In contrast, adult sporophytes are generally exposed to wider ranges of light conditions. Due to their large size these plants "escape" from some these detrimental constraints.

In contrast to I_k, low light requirements for compensation of photosynthesis (I_c) of Antarctic macroalgae seem to be a very conservative character. In general, culture plants from several species exhibit I_c values $\leq$ 10 µmol photons m^{-2} (Wiencke et al. 1993, Gómez et al 1995a,b, 1996, Wiencke 1997a) and suggest a direct relation with the minimum light requirements for growth. In *Desmarestia menziesii*, a species with strong seasonal changes in I_k values, I_c remains constant and with values below the culture irradiances (Gómez & Wiencke 1997a). These results suggest that saturation of photosynthesis is not necessarily a metabolic pre-requisite for growth. According to Henley (1993), net C assimilation still ocurrs below the I_k point probably enough to support growth of macroalgae. This is not

often taken into account in productivity models. If light is not limiting, then high respiration rates might not affect C balance. Thus, maintaining an I_c always below the ambient irradiance would be an advantage to achieve positive net C assimilation (high P/R ratios) during periods of maximum growth. This situation is supported by I_c values from field plants, which generally are higher than in cultured plants, but are lower than prevailing *in situ* irradiances during spring (Klöser et al. 1993, Gómez & Wiencke 1997a).

7. PHOTOSYNTHETIC CHARACTERISTICS IN RELATION TO DEPTH ZONATION

7.1. Multi-specific responses

Antarctic macroalgae are mostly subtidal organisms. Despite this well known fact, few efforts have been made to explain zonation patterns in terms of physiological characteristics. Although due to the action of different environmental factors e.g. ice-cover, phytoplankton blooms, or water turbidity due to melt water light penetration is constrained during a great part of the year, algae are able to grow at large depths (Zielinski 1981, 1990, Klöser et al. 1993,1994). Much of the available data characterise Antarctic shallow waters as extremely transparent (Bienati & Comes 1971, Priddle et al. 1986), particularly during late-winter spring. Under such conditions, macroalgae can potentially occur at depths close to 40 m as inferred from I_c and I_k for photosynthesis of cultured material (Wiencke et al. 1993, Gómez et al. 1995a, b, 1996, Gómez & Wiencke 1996). The hypothesis that light requirements for photosynthesis of Antarctic macroalgae may be related to their actual zonation patterns has primarily been tested using a large spectrum of species collected from of different depth levels at King George Island (Weykam et al. 1996).

Figure 11 summarizes the photosynthetic performance and light requirements for saturation of photosynthesis in 36 species belonging to the green, red and brown algae. Although algae from shallow waters or intertidal locations (green and some brown algae) show higher net P_{max} and I_k than species from deeper habitats, no evidence for a marked adaptation of algae to depth can be demonstrated. In general, net P_{max} (**Fig. 11A**) is similar (< 25 μmol O_2 g^{-1} FW h^{-1}) and not depth-related in most red and brown algae, however, species such as *Desmarestia antarctica*, *Geminocarpus geminatus* and *Phaeurus antarcticus* from depths between 1 and 3 m have very high P_{max} values (75 to 125 μmol O_2 g^{-1} FW h^{-1}) only comparable to values measured in the intertidal green alga *Urospora*

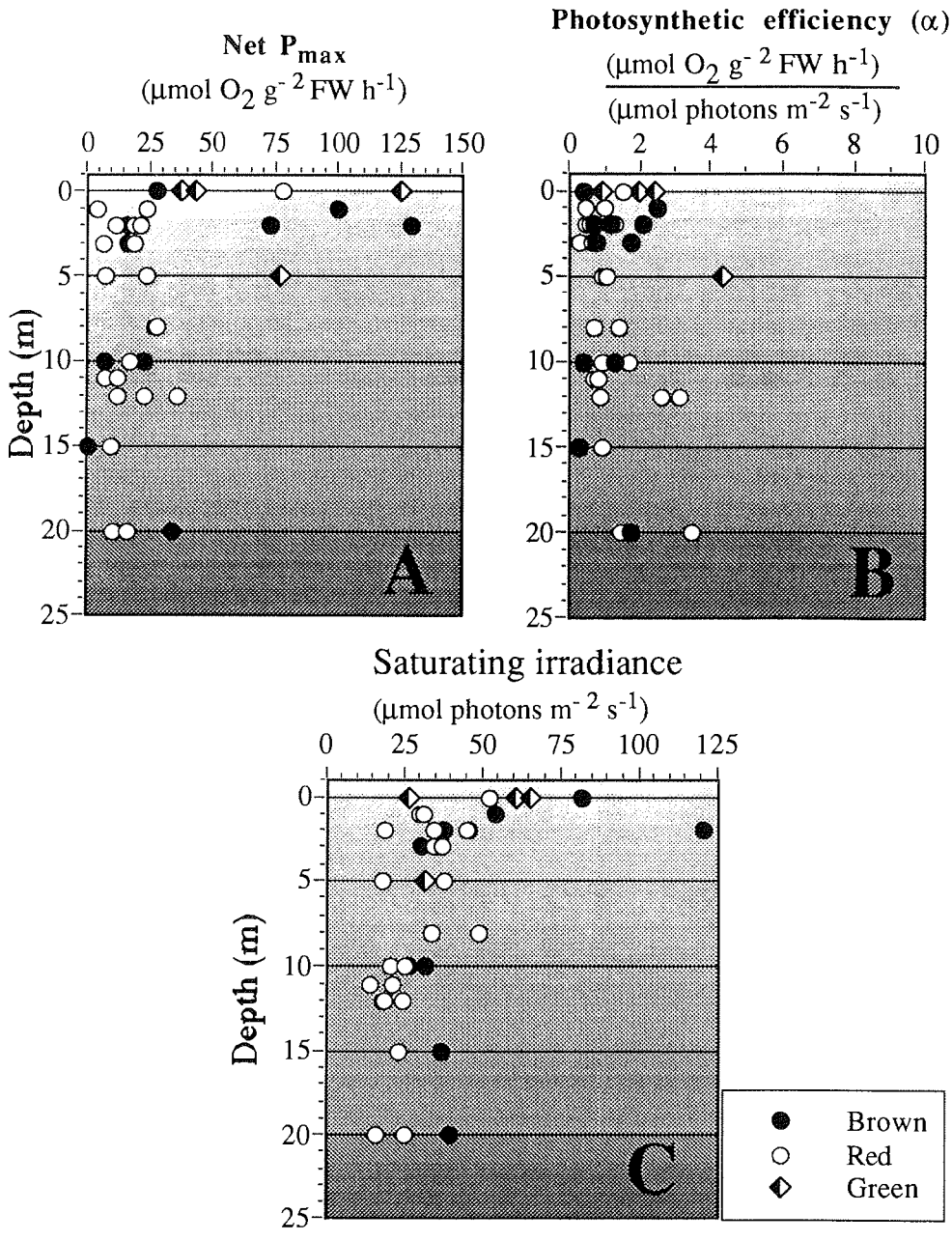

Fig. 11. Changes in photosynthetic parameters A) net P_{max}, B) α and C) I_k of brown, red and green algae collected at different depths in King George Island (spring-summer 93/94). Re-drawn from Weykam et al. 1996.

penicilliformis and the Chrysophyte *Antarctosaccion applanatum*. In contrast, the photosynthetic efficiency (α, **Fig. 11B**) shows no obvious differences at all between species groups with values ranging between 0.25 for *Cystosphaera jacquinotii* and 4.3 µmol O_2 g^{-1} FW h^{-1} (µmol photon m^{-2} s^{-1})$^{-1}$ for *Antarctosaccion applanatum* with 80 % of the species exhibiting values $\leq$ 2 µmol O_2 g^{-1} FW h^{-1} (µmol photon m^{-2} s^{-1})$^{-1}$. At depths between 12 and 20 m, red algae (generally understorey species) exhibit the highest α values.

Like net P_{max}, only I_k values of some species collected between 0 and 3 m depth are high (**Fig. 11C**), agreeing with previous results found in culture plants (Wiencke et al. 1993). Interestingly, the highest I_k values were determined in the shallow water brown algae *Phaeurus antarcticus* and *Adenocystis utricularis* (125 and 81 µmol photon m^{-2} s^{-1}, respectively), whereas the lowest ones (between 14 and 50 µmol photon m^{-2} s^{-1}) were found in the red algae collected over a long vertical range. These ranges are in agreement with incident irradiances measured *in situ* at King George Island (Klöser et al. 1993, Gómez et al. 1997a). In terms of physiological properties, these data allow to partially elaborate a pattern of macroalgal zonation. In general, macroalgae growing at large depths, exhibit, irrespective of the algal division, low I_k values, however, photosynthesis of species from shallow waters can also be saturated at comparably low irradiances. On the other hand, the highest I_k values might be expected in macroalgae growing in shallow waters. Low light requirements for saturation of photosynthesis of species living at supralittoral and upper sublittoral levels are also reported by other macroalgal assemblages from temperate regions and may primarily be related to low light requirements for growth (Orfanidis 1992, Leukart & Lüning 1994). Finally, it may be speculated that the ability to grow and photosynthesize under low irradiances is a common characteristic in the Antarctic macroalgae, probably genetically fixed and independent of the growth depth. Thus, shade adaption in these species may have evolved in response to the seasonally fluctuating light availability and the long exposure to low light or dakness in

winter, thereby in parallel allowing algae to amplify their depth distribution limits.

7 2. Intra-specific patterns

A striking characteristic of the sublittoral zonation of Antarctic macroalgae is the marked dominance of certain species of brown algae (DeLaca 1976, Richardson 1979, Klöser et al. 1994, Amsler 1995, Brouwer et al. 1995). Recently, Klöser et al. (1996) defined a pattern of zonation characterised by four principal zones: a supralittoral, dominated by small chlorophytes and benthic diatoms, an upper sublittoral dominated by *Desmarestia menziesii* and *Ascoseira mirabilis* subject to strong wave impact, an intermediate fringe inhabited by *Desmarestia anceps* exposed to moderate wave action and finally a calm, deeper zone dominated by *Himantothallus grandifolius*. Other species such as some red algae (*Gigartina*, *Palmaria*) occupy open gaps between the brown algal canopy. The structure and persistence of this zonation scheme is strongly modified by ice-abrasion, and probably also by grazers, e. g. some invertebrate and demersal fishes (Iken 1996, Iken et al. 1997). In contrast to the algal zonation patterns from other geographical regions, where dominant species generally form narrow belts (see Lüning 1990), vertical distribution of dominant Antarctic macroalgae such as *Desmarestia* or *Himantothallus* can become very extended (Klöser et al. 1996). Intuitively, such patterns firstly suggest that these species have high acclimation potential of photosynthesis to the various light climates over the depth gradient. However, a relationship between photosynthetic capacity and depth has only been partially demonstrated (Gómez et al. 1997a). Using O_2-based photosynthetic measurements, only erratic changes in net P_{max} were found in the brown algae *Desmarestia menziesii* and *Himantothallus grandifolius* and in the red algae *Kallymenia antarctica*, *Gigartina skottsbergii* and *Palmaria decipiens* with increasing depth. Similarly, α values reveal no evidence for an enhanced light use of plants collected at 30 m depth compared to plants from 10 and 20 m. These

data are supported by scarce variations in Chl *a* contents with depth. Only *Himantothallus grandifolius* shows increasing α values and Chl *a* contents with increasing depth. Overall, these findings indicate no photoacclimation of macroalgae in terms of photosynthetic O_2 production both at saturating and sub-saturating irradiances. These results can be interpreted in various ways. Firstly, the high light penetration during the study period does not limit irradiance for photosynthesis (see discussion below). Secondly, absence of depth-dependent variations in α values may be related to the thick (leathery and terete) thallus structure of the studied species leading to negligible variations in thallus-specific pigment contents (Markager 1993). Because no evidence for changes in thallus morphology for a single species with depth has been demonstrated up to now, it is possible to argue that the relation surface area/volume *vs* Chl *a* contents remains constant and sets the optimum light utilization in these plants over a broad range of vertical zonation. Finally, slight decreases in Chl *a* in plants of *Kallymenia antarctica*, *Palmaria decipiens* and *Gigartina skottsbergii* collected at 30 m depth might be linked to relative increases of accessory pigments such as phycobilins (not measured). Therefore the relative proportion of the Chl *a* to the total light absorption capacity of the plants at low light decreases and consequently higher α values on a Chl *a* basis may be expected (Kirk 1994).

As has been outlined previously, Antarctic macroalgae are shade-adapted organisms, a characteristic which evolved probably in response to the seasonal fluctuations in light availability. Thus, the low light requirements for photosynthesis may confer additional advantages to penetrate to deeper, less well illuminated habitats. Under optimum conditions in the Antarctic spring-summer, water transparency allows average irradiances close to 20 μmol photons m^{-2} s^{-1} at 30 m, with 1 % surface irradiance at depths larger than 40 m (Gómez et al. 1997a). Although these levels are clearly lower than average midday irradiances (30 to 325 μmol photon m^{-2} s^{-1}) at 30 m in some clear temperate coasts and tropical waters (Peckol & Ramus 1988), they exceed reported saturation and compensation points of photosynthesis in most Antarctic macroalgae studied so far

(**Table 8**). Despite some discrepancies in I_c values between different studies of the same species, the I_c values of plants from 30 m appear to indicate the minimum light requirements for photosynthesis in these species. In the particular case of *Himantothallus grandifolius* and the red algae *Palmaria decipiens* and

Table 8. Light requirements for saturation (I_k) and compensation (I_c) of photosynthesis of Antarctic macroalgae collected at different depths. *In situ* depth irradiances for King George Island taken from Gómez et al. 1997a.

Species	Location	Depth (m)	*In situ* irradiance	I_k	I_c	Reference
			(μmol photon m^{-2} s^{-1})			
Brown algae						
Himantothallus grandifolius	Signy Island	5-10	75-17		30	Drew (1977)
	King George I.	10	264	26.5 (3.3)	8.1 (0.8)	Weykam et al. 1996
	King George I.	10	264	29.3 (2.9)	9.8 (1.2)	Gómez et al. 1997a
	King George I.	20	85	25.7 (5.9)	5.9 (0.6)	Gómez et al. 1997a
	King George I.	30	21	22.4 (2.2)	6.4 (0.5)	Gómez et al. 1997a
Ascoseira mirabilis	King George I.	3	700	35.6 (6.2)	13.3 (2.0)	Weykam et al. 1996
Desmarestia anceps	Signy I.	1-10	200-17		15	Drew (1977)
	King George I.	10	264	32.1 (3.1)	15.5 (1.1)	Weykam et al. 1996
	King George I.	10	264	58.0 (8.2)	26.6 (1.4)	Gómez et al. 1997a
	King George I.	20	85	31.7 (4.3)	7.9 (0.4)	Gómez et al. 1997a
	King George I.	30	21	44.3 (5.7)	20.6 (0.5)	Gómez et al. 1997a
	Signy I.	5-22	n.d	14.6 (1.9)	1.04	Brouwer (unpub)
Desmarestia antarctica	Signy I.	1-10	700-17		20	Drew (1977)
	King George I.	2	780	38.0 (13.3)	11.0 (5.3)	Weykam et al. 1996
Red algae						
Palmaria decipiens	Signy I.	1-10	200-17		15	Drew (1977)
	King George I.	8	346	48.6 (5.7)	5.7 (0.8)	Weykam et al. 1996
	King George I.	10	264	36.8 (8.8)	10.4 (2.3)	Gómez et al. 1997a
	King George I.	20	85	41.5 (6.1)	6.7 (0.5)	Gómez et al. 1997a
	King George I.	30	21	18.6 (5.6)	5.8 (2.4)	Gómez et al. 1997a
Gigartina spp.	Signy I.	1-10	200-17		15	Drew (1977)
Gigartina skottbergii	King George I.	10	264	31.4 (3.9)	3.9 (1.7)	Gómez et al. 1997a
		20	85	14.4 (4.1)	1.0 (0.4)	Gómez et al. 1997a
		30	21	15.5 (2.2)	1.6 (1.2)	Gómez et al. 1997a

Gigartina skottbergii from King George Island, respiration is compensated by photosynthesis at irradiances between 1.6 and 6.4 μmol photon m^{-2} s^{-1}, corresponding to 8 and 30 % of the average irradiance at this depth (Gómez et al. 1997a). In general, these values are comparable to I_c values between 3 and 9 μmol photon m^{-2} s^{-1} reported in several *Laminaria* species including the Arctic *L. solidungula* (summarized in Dunton & Jodwalis 1988). Although Drew (1977) reported higher I_c values for *Palmaria decipiens*, *Gigartina* spp., *Desmarestia menziesii* closely matching minimum ambient irradiances at only 10 m depth (17 μmol photon m^{-2} s^{-1}), these values are significantly lower than compensating irradiances of 18 subtidal Mediterranean macroalgae (mean 57.9 μmol photon m^{-2} s^{-1}; Enriquez et al. 1995).

The use of minimum light requirements for photosynthesis (I_c in this case) to predict maximum depth penetration of macroalgae has been recently challenged as both I_c values for photosynthesis and I_c values for growth estimate related but not identical physiological properties (Markager & Sand-Jensen 1992). This discrepance is explained by the close relationships between dark respiration and growth rates. Dark respiration rates increase with growth, which causes also increases of I_c for photosynthesis. In contrast, the more active the growth activity, the lower is I_c for growth. Therefore, I_c values for photosynthesis are always higher than I_c for growth. For example, *Laminaria solidungula* had an I_c for growth close to 0.6 μmol photon m^{-2} s^{-1} (Chapman & Lindley 1980), whereas its I_c for photosynthesis increases to 3 μmol photon m^{-2} s^{-1} (Dunton & Jodwalis 1988). Similarly, Orfanidis (1992) reported I_c for growth of Mediterranean macroalgae ranging between 0.5 and 1 μmol photon m^{-2} s^{-1}, contrasting substantially with the above reported I_c for photosynthesis (Enriquez et al. 1995). For Antarctic macroalgae, no estimations of I_c are available for comparisons, however, extrapolated minimum requirements for growth from irradiance-growth curves reported by Wiencke (1990a) and Wiencke & Fischer (1990) indicate that macro- and microthalli of several brown algae can grow at

irradiances < 1 μmol photon m^{-2} s^{-1}. On the basis of these results, Antarctic macroalgae would possess the metabolic capacity to penetrate and eventually colonize depths between 30 and 40 m, especially the early establishment phases in virtue of their ability to use very low irradiances (Wiencke 1990a, Gómez & Wiencke 1996).

7. 3. Light availability and carbon balance

Growth of macroalgae at deep habitats is achieved by an efficient use of low irradiances for photosynthesis, i. e., optimal conversion of light energy to assimilated carbon, and also by reducing carbon losses due to respiration (Markager 1993). If the effects of other physical factors such as wave (or ice) abrasion or losses of tissues caused by grazers, excretion of organic substances, are not present, light requirements for photosynthesis are primarily set by the vertical growth limits of the algae and consequently can be used to estimate productivity (Matta & Chapman 1991). Studies conducted in seagrasses show that variations in the photosynthesis/respiration ratios on a daily basis (daily carbon balance) can be considered as a physiological indicator of depth suitability (Dennison & Alberte 1982,1985). In principle, this model compares the relative effects of intensity of quantum irradiance and duration of daily exposure to these irradiances on photosynthesis. The key elements defining a productivity model of this type are the daily light course of the irradiance and the saturation point for photosynthesis (I_k), which determine the daily period for which plants are exposed to irradiances ≥ I_k, denominated H_{sat}. Polar macroalgae exposed to marked seasonal changes in daylength exhibit generally $H_{sat} > 0$ h only during the short open water season. *Laminaria solidungula* in the Alaskan High Arctic, which exhibit an average I_k of 38 μmol photon m^{-2} s^{-1} (Dunton & Jodwalis 1988), was exposed during August to September 1986 to total H_{sat} periods of up to 148 h. This value corresponds to an extrapolated daily H_{sat} of 3 h. However, depending on the year, H_{sat} may become as low as 39 h during these months, i. e., an extrapolated daily H_{sat} < 0.5 h, which was correlated to low carbon allocation

(Dunton 1990). For Antarctic macroalgae, H_{sat} measured during optimum light conditions in spring in five brown and red algae generally decreases with depth from values close to 14 h at 10 m to values between 7 and 12 h at 30 m depth (Gómez et al. 1997a). These values are comparable to ranges of H_{sat} between 7.2 and 13.3 h determined in the temperate *Colpomenia peregrina* from subtidal (3 m) populations (Matta & Chapman 1991). Such similarities reflect the ability of Antarctic macroalgae to efficiently use low light as *C. peregrina* plants are exposed to midday irradiances close to 400 and 800 μmol photon m^{-2} s^{-1} in winter and summer respectively, with I_k values mostly > 100 μmol photon m^{-2} s^{-1}. In Antarctic macroalgae, photosynthesis of plants growing between 10 and 30 m depth is saturated at significantly lower irradiances (**Table 8**). Species such as the red algae *Palmaria decipiens* and *Gigartina skottbergii* have very low I_k-values of 18 and 15 μmol photon m^{-2} s^{-1}, somewhat lower than *in situ* irradiances measured at 30 m depth (close to 20 μmol photon m^{-2} s^{-1}; Gómez et al. 1997a). For the brown algae *Himantothallus grandifolius* and *Desmarestia menziesii* collected at 30 m, these authors reported I_k close to 22 and 44 μmol photon m^{-2} s^{-1}, respectively. Interestingly, I_k of these species do not increase markedly with increasing depth: I_k values of 26 and 32 μmol photon m^{-2} s^{-1} measured at 10 m, clearly are below the irradiances measured at this depth (> 200 μmol photon m^{-2} s^{-1}). The reasons why algae growing under non limiting ambient irradiance in spring maintain low I_k and I_c values seem to be accounted by the fluctuating irradiance input in the Antarctic. Firstly, most of the Antarctic brown algae are perennial organisms with a high longevity, thus constant low light requirements would ensure the survival and biomass formation under a wide variety of light climates. Secondly, low light requirements for photosynthesis may be favourable at shallow sites when extra and/or intra specific canopy effects limit incident light. This is especially evident in red algae, which generally attain a smaller size than brown algae and show understorey characteristics.

As outlined above, sublittoral macroalgae have developed metabolic strategies to maximize carbon fixation avoiding excessive carbon losses due to

respiration. Because at great depths, I_c for photosynthesis exceed I_c-values for growth and available irradiances are normally below the levels required for saturation of photosynthesis, carbon assimilation may be just compensating dark respiration. In the studied Antarctic brown algae, dark respiration has a strong seasonal component and during the growth period, respiratory activity may account for a considerable proportion of the gross photosynthesis (Gómez et al. 1995b, 1997a,b). As dark respiration is assumed to occur over the 24 h period and light carbon fixation only during the H_{sat} period, a positive daily carbon balance indicates the light conditions at which growth may be possible. In this sense, productivity of Antarctic macroalgae appears to be constrained at depth > 30 m (Gómez et al. 1997a). For the red algae *Palmaria decipiens*, *Kallymenia antarctica* and *Gigartina skottsbergii* metabolic carbon balance between 0.6 and 0.8 mg C g^{-1} FW d^{-1} at 30 m sets the limits for growth. At upper subtidal levels, carbon balance increases significantly (values up to 3.5 mg C g^{-1} FW d^{-1}). In the case of the brown alga *Himantothallus grandifolius*, which dominates depths below 15 m, daily carbon balance was low but relatively similar over a range between 10 and 30 m, which may be related to the massive morphology of this species. *Desmarestia anceps* growing at 20 m shows a high productivity comparable to red algae, but at 30 m, growth of this species is clearly limited due to its negative carbon balance (-1.9 mg C g^{-1} FW d^{-1}; Gómez et al. 1997a). On the basis of these results, it may be argued that *Desmarestia anceps* is not well suited to grow at large depths and therefore other factors, such as the use of storage carbohydrates or a high rate of light-independent carbon fixation supports in part metabolic activity. Conversely, red algae are metabolically able to grow at large depths, however, they are outcompeted by the large canopy brown alga *Himantothallus* and eventually *Desmarestia* species (Klöser et al. 1996). At any case, daily carbon balance may be considered a good indicator of the potential capacity of macroalgae to grow (under spring conditions) over a broad vertical gradient in the Antarctic. It is, however, not clear whether macroalgae persist at these depths during winter, when light dramatically decreases, or penetration at large depth is

only a spring-summer phenomenon. Further studies are required to clarify more accurately the effects of other physical and biological factors on the zonation of these plants.

8. ORGANIC COMPOSITION

With the exception of some short reports (Czerpak et al. 1981, Dhargalkar et al. 1987, Gómez & Westermeier 1995), changes in organic constituents and their role on the physiology of Antarctic macroalgae are poorly known. This lack of information contrasts with the abundant data on cold-temperate seaweeds, specially brown algae, from the northern Hemisphere, where changes in organic compounds have been recognized as key components of the morpho-physiological processes in these plants (Chapman & Craigie 1978, Gerard 1982, Gagné et al. 1982, Schmitz 1981, Henley & Dunton 1995). The complex morphologies and seasonal growth patterns of Antarctic brown algae, intuitively underly corresponding changes in allocation of the major organic constituents. Moreover data on organic composition in these species may be useful to estimate nutrient balance and energy exchange in the whole coastal system. As was reported by Zielinski (1981) for Admiralty Bay, King George Island, 279 tons dry algal matter (123 ton of brown algae) are deposited along 15.8 km shore line during a period of 10 months. Due to decomposition, 27 % (75 tons) of the algal debris is released as organic and mineral matter back into the water mass in an average time of 12 days. Based on these quantities, it is clear that macroalgae are important contributors to the organic matter circulation not only in shallow but also in deep bottoms as was demonstrated also by the ocurrence of abundant macroalgal debris at depths close to 2000 m (Fischer & Wiencke 1992).

The present section will focus on the organic composition in Antarctic macroalgae with particular emphasis on morpho-functional relations and seasonal variations. Early and recent information will be confronted to generate a picture of the advances and to outline some aspects requiring future investigation.

8.1. Nitrogen contents

Tissue N composition is an indicator of ambient nutrient availability and for the N requirements for growth in macroalgae (Hanisak 1979, Lapointe & Tenore

1981, Fujita 1985). The finding that low ambient NO_3 concentrations during spring and summer limit growth of kelps from cold temperate and Arctic regions has dominated for almost three decades the discussion about the environmental factors affecting productivity in macroalgae (Black 1954, Buggeln 1978, Chapman & Craigie 1977, 1978, Gerard 1982, Gagné et al. 1982, Asare & Harlin 1983, Zimmerman & Kremer 1986, Hein et al. 1994). In contrast, aspects concerning N uptake, storage and N-related growth in the large Antarctic brown algae have been poorly studied. A reason for this may be the high and constant NO_3 concentrations (the most important N source) reported for Antarctic waters, which may have stopped scientists to work on this question. Long term measurements carried out in Signy Island (Drew & Hastings 1992) reveal low seasonal changes in NO_3 concentrations averaging 20 µM throughout the year, while in some protected bays of King George Island (Admiralty Bay), maximum nitrate concentrations can exceed 33 µM (Lipski 1987). Although phytoplankton blooms after ice-cover break up can locally deplete NO_3 (minima slightly lower than 10 µM; Drew & Hastings 1992), these values are clearly higher than dissolved inorganic N necessary for supporting the growth of kelps. Chapman et al. (1978) reported that growth of *Laminaria saccharina* from the North Sea (Helgoland) was limited at NO_3 concentrations below 10 µM. This seems to be an exceptional situation since much of the kelp assemblages are exposed to NO_3 concentrations rarely exceeding 10 µM (Gagné et al. 1982, Asare & Harlin 1983, Sjøtun et al. 1996). In the Alaskan High Arctic, maximum NO_3 concentrations close to 3 µM (almost 10 times lower than Antarctic records!) support growth of *Laminaria solidungula* during darkness in winter (Dunton & Schell 1986). Other kelps such as *Macrocystis pyrifera* grow also under low ambient NO_3 concentrations, in both north Pacific (California) and south Atlantic (Falkland Islands) populations (Wheeler & North 1981, van Tussenbroek 1989). According to estimations of Gerard (1982), growth of this species would be limited at NO_3 levels below 2 µM.

If one assumes a direct relationship between dissolved N concentration and tissue N content, then considerably higher internal N contents in Antarctic macroalgae may be expected compared to species from other regions. However, this situation does not appear to be a rule. **Table 9** compares N contents between the major Antarctic brown algae and temperate, cold-temperate and Arctic members of the Laminariales. Although N contents > 4 % DW are found in species such as *Himantothallus grandifolius*, *Desmarestia menziesii* and *Ascoseira mirabilis* during spring-summer, values < 2 % DW are, on a seasonal basis, not uncommon and are lower than maximum N contents measured in species such as *Laminaria longicruris* (Chapman & Craigie 1978), *Macrocystis pyrifera* (Wheeler & North 1981, van Tussenbroek 1989) and *Macrocystis integrifolia* (Rosell & Srivastava 1985). However, when minimum values in summer are considered, cold-temperate and Arctic kelps exhibit very low tissue N content close to or lower than 1 % DW, reflecting clearly the low ambient N levels. Such low N contents in summer are common for these species, but not in Antarctic brown algae. For example, tissue N contents in *Ascoseira mirabilis* are high in early spring when active growth takes place and low in summer (Gómez & Wiencke 1997b), whereas in *Desmarestia menziesii,* the reversed seasonal pattern is observed (Gómez et al. 1997b). An explanation for this situation is not easy. It is, however, likely that uptake and later use of nitrogen in these species are different as both have different morphological structure and probably distinct energy requirements for growth. In this sense, it was reported that filamentous and foliose morphologies have significantly higher N contents than terete and leathery algae from King George Island (Weykam et al. 1996), which may be related to differences in intrinsic growth rates. Whereas in delicate and small algae, increased allocation of energy per unit weight involve also high N requirements, large and complex macroalgae experience a more slow growth and consequently lower tissue N contents can be expected (Pedersen & Borum 1996).

However, irrespective of the thallus morphology, minimum tissue N contents of Antarctic macroalgae are always ≥ 1.8 % DW. If the critical N

Table 9. Comparison of C and N contents (% DW) and C/N ratios among Antarctic, cold-temperate and Arctic brown algae. Values are minima and maxima reported in each study. Abreviations in parentheses indicate the season when material was sampled. Wi = winter; Sp = spring; Su = summer; Au = autumn; Ann = annual average.

Species	Location	N	C	C/N ratios	Reference
Cold-temperate:					
Macrocystis integrifolia	Vancouver Island (Canada)	1.3 (Su)- 2.7 (early Wi)	26 (early Wi)- 30 (Au)	9.9 (Sp)- 37(Su)	Rosell & Srivastava (1985)
Saccorhiza polyschides	Port Erin (Isle of Man)	1.5 (Su)- 2.3 (Sp)	20.2 (Sp)- 24.0 (Su)		Jensen et al. (1985)
Laminaria longicruris	Nova Scotia (Canada)	1.0 (Aut)- 4.2 (Sp)			Chapman & Craigie (1978)
Laminaria saccharina	Rhode Island (Camp Varnum)	0.9 (Su)- 2.3 (Wi)	24 (Su)- 35 (Sp)		Asare and Harlin (1983)
Macrocystis pyrifera	Laguna Beach (California)	1.1-2.6 (Wi)			Gerard (1982)
	Southern California	1.0 (Su)-3.7 (Wi)	23 (late Wi)- 27 (Sp)	10 (late Wi)- 27 (Au)	Wheeler & North (1981)
	Falkland Islands (Stanley Harb.)	< 1 (Su)- 3.3 (Wi)	25 (Wi)- 30.5 (Su)	7 (Wi)- 47 (Su)	van Tussenbroek (1989)
Arctic:					
Laminaria saccharina	Alaskan High Arctic	2 (Su)- 3 (Sp)		13 (Sp-Su)	Henley & Dunton (1995)
	West Coast Norway	< 1 (Su)- 2.5 (Wi)	20 (Wi)- 36 (early Au)		Sjøtun (1993)
Laminaria solidungula	Alaskan High Arctic	1.4 (Sp)- 2.7 (late Su)	26 (Sp)- 37 (Wi)		Dunton & Schell (1986)
	Alaskan High Arctic		28 - 35 (Ann 1988-84)		Dunton (1990)
	Alaskan High Arctic	1.9 (Su)- 2.3 (Sp)	27 (Sp-Su)	13 (Sp)- 15 (Su)	Henley & Dunton (1995)
Antarctic:					
Himantothallus grandifolius	King George Island	1.8 (Su)		10.1 (Su)	Czerpak et al. (1981)
	Vestfold Hill (East Antarctica)	2.0 (Su)	30.4 (Su)	14.9 (Su)	Dhargalkar et al. (1987)
	King George Island	5.5 (Su)	34.7 (Su)	15.2 (Su)	Weykam et al. 1996
Desmarestia menziesii	Vestfold Hill (East Antarctica)	1.8 (Su)	34.2 (Su)	18.1 (Su)	Dhargalkar et al. (1987)
	King George Island	4.5 (Su)	28.3 (Su)	7.3 (Su)	Weykam et al. 1996
	King george Island	3.6 (Sp)-4.6 (Su)	31.2 (early Sp)- 42.9 (Su)	8.2 (early Sp)- 9.7 (Su)	Gómez et al. 1997b
Desmarestia anceps	King George Island	3.3 (Su)	32.8 (Su)	10.1 (Su)	Weykam et al. 1996
Ascoseira mirabilis	King George Island	3.1 (early Sp)- 1.8 (Su)	30 (Sp)- 36 (early Su)	12.2 (Sp)- 20.5 (Su)	Gómez & Wiencke 1997b
	King George Island	4.4 (Su)	32.8 (Su)	10.5 (Su)	Weykam et al. 1996

content of 1 % DW, defined by Asare & Harlin (1983) as the limit between depletion and storage of nitrate in *Laminaria*, is invoked, then Antarctic macroalgae are always oversaturated of N. Interestingly, tissue N levels in some Antarctic macroalgae are not constrained by light limitation at depths between 10 and 30 m (Gómez et al. 1997a). All these findings would confirm that growth in these algae is not triggered by N levels and seasonal changes in growth are dependent on seasonal daylength variations and photoperiodism or circannual rhythms as suggested by Lüning (1991). However, because of the limited body of experimental evidence, no conclusive interpretations can be outlined.

8.2. Carbon content and biomass allocation in the thallus

Total organic carbon contents have been frequently used in models predicting growth, biomass allocation and energy requirements in several organisms (reviewed in Gnaiger & Bitterlich 1984). In macroalgal ecology, however, such approaches are of recent origin and respond to a necessity of finding accurate parameters describing thallus growth and other physiological processes (Markager & Sand-Jensen 1996). In contrast tissue N contents, C contents in large brown algae vary little with species and do not show a defined seasonal pattern (**Table 9**). Species such as *Saccorhiza polyschides* may be regarded as an example for algae having low values varying between 20 and 24 % C (Jensen et al. 1985), but in general, *Laminaria* species, irrespective of their geographical distribution show C contents ranging betwen 24 and 37 % DW (Asare & Harlin 1983, Rosell & Srivastava 1985, Dunton 1990, Sjøtun 1993). For Antarctic species, C contents between 28 and 43 % DW (measured generally in spring-summer; Dhargalkar et al. 1987, Weykam et al. 1996, Gómez & Wiencke 1997b, Gómez et al. 1997b) are comparable to corresponding values of cold-temperate and Arctic kelps (Henley & Dunton 1995). Whether these values decrease in winter, is not clear due to the lack of winter measurements.

In terms of morpho-functional variations, it has been demonstrated that dry weight-based C contents of filamentous and foliose algae are significantly higher

than those measured in terete and leathery species (Weykam et al. 1996). This clearly does not agree with the expected higher allocation of biomass per weight unit in species with thick morphologies compared to delicate forms often reported for temperate species (Khailow 1976, Littler & Littler 1980). These patterns are also confirmed when the C content is recalculated as a function of the surface area. For a thin sheet like alga such as *Porphyra endiviifolium*, a high thallus specific C contents (TSC) close to 3 mol C m^{-2} can be calculated, whereas in leathery species such as *Ascoseira mirabilis*, *Himantothallus grandifolius* or *Kallymenia antarctica*, TSC may decrease to values close to 1.4 and 1.8 mol C m^{-2}. This contrasts with models proposed by Markager & Sand-Jensen (1996), who report thallus specific C contents (TSC) of 4 and 6 mol C m^{-2} in leathery species such as *Chondrus crispus* and *Fucus serratus* significantly higher than TSC values measured in the delicate algae *Ulva lactuca* and *Petalonia fascia* (between 0.3 and 0.9 mol C m^{-2}). The high thallus density and the high proportion of dry weight of *Porphyra endiviifolium* from Antarctica, contrasting with leathery plants characterized by high water contents (Weykam et al. 1996), may account for such discrepances. Undoubtedly, TSC is affected by the proportion of total organic C effectively allocated in metabolic or structural compounds (Duarte 1992). In general large brown algae, including Antarctic species, show both lower bomb calorimetric and C-based calorific values than smaller species (Himmelmann & Carefoot 1975, Dhargalkar et al. 1987, Gómez & Westermeier 1995), suggesting a direct relationship to metabolic activity. On the other hand, high C contents per surface area are unlikely to be a species-specific characteristic as seasonal changes in TSC have been reported in *Ascoseira mirabilis* (Gómez & Wiencke 1997b). In this species, TSC measured in basal blade regions shows seasonal changes closely correlated to net photosynthesis and α values indicating that TSC, a biomass parameter, affects the light use characteristics of the thallus as has been also proposed by Markager & Sand-Jensen (1996).

Seasonal changes in C contents, biomass allocation and thallus morphology may also be related to changes in C acquisition. Wiencke & Fischer (1990) found

a close relation between growth rates, light intensity and stable C isotope composition in Antarctic macroalgae grown under laboratory conditions. Results in $^{13}C/^{12}C$ ratios measured in field plants of *Ascoseira mirabilis* (unpublished data) agree to some extent with these findings. High isotopic ratios (between -12 and -16 δ ‰ PDB) were measured in all regions of the blade in December when the algae are exposed to high irradiances and daylengths (close to 19:5 L:D). The reasons explaining this pattern may be multiple and in many cases involve internal and external factors. For example a lower ^{13}C discrimimation under high light conditions has been related to a ^{12}C depletion caused either by ambient CO_2 depletion or by increased C uptake, leading to a preferential assimilation of the heavier C isotope (Wiencke & Fischer 1990, Raven et al. 1995). The CO_2 *vs* HCO_3 utilization as C source has also been defined as a major factor determining internal $\delta\,^{13}C$ in macroalgae. Under normal conditions, inorganic ^{12}C (CO_2) is preferentially assimilated due to its greater diffusion rate, however, ^{13}C may be incorporated at high rates when active transport of HCO_3 takes place. Therefore under high light availability, the higher photosynthetic and consequently high carboxylation rates, compensate for the energy costs of active HCO_3 incorporation decreasing the C supply via diffusive CO_2 entry (Raven 1970, Kübler & Raven 1994). Moreover, there may be also combined effects of plant size, plant age and changes light use efficiency. In culture plants of *Desmarestia menziesii* (**Fig. 12**), values > -29 are found in plants with fresh weight lower than 6 g, but with increasing size (10 g FW), $^{13}\delta$ values decrease accordingly (-32 ‰ PDB). In this sense, Raven *et al* (1995) stressed the importance of the HCO_3 utilization (and eventually ^{13}C incorporation) in macroalgae indicating that CO_2 diffusion and its fixation by RUBISCO (ribulose bisphosphate carboxylase oxygenase) is favoured in habitats characterized by low light, due to lower metabolic activity of the algae. In our case, the increased ^{13}C discrimination during December and February does not fit to a higher light availability (longer daylengths) but agrees with a possible effect of decreased metabolic activity in plants with increasing age and size.

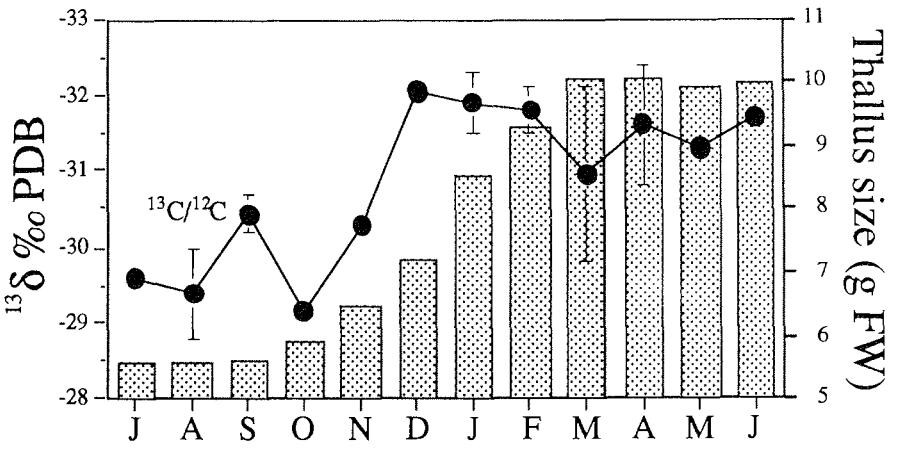

Fig. 12. Seasonal changes in $^{13}\delta$ discrimination as a function of thallus size (weight) in *Desmarestia menziesii* cultured under seasonally fluctuating daylengths.

Although these data constitute the first reports asssessing seasonality of biomass using TSC, C-based energy contents and isotope C composition of Antarctic macroalgae, no definitive conclusions about its implications on the photosynthetic metabolism could be outlined and further investigations are indispensable here.

8.3. Major organic constituents and role of storage carbohydrates

Seasonal changes in major organic compounds, e.g. proteins, amino acids, lipids, and carbohydrates in macroalgae are known since 40 years and were based on studies of large brown algae, especially Laminariales (Black 1948, 1950, Haug & Jensen 1954, Jensen & Haug 1956). Although most of the patterns found were related to gradients of environmental variations (salinity, temperature, light, etc.), no questions relating life strategy, morpho-functional processes and environmental effects were addressed by these early investigators. Only after the classic works by Chapman & Craigie (1977, 1978), a relatively comprehensive picture of the relationship between growth and organic composition in *Laminaria* species was available. Hatcher et al. (1977) indicated that thallus C and N budget

are closely related and determine the seasonal strategy of growth of *Laminaria longicruris*. Basically, degradation of storage carbohydrates built up in summer (when photosynthetic C assimilation exceeds C utilization), supply the energy requirements for growth during high N availability in winter-early spring when either negligible or no photosynthesis takes place. However, large brown algae exhibit also a complex morphological architecture and a specialized internal functional organization leading to a spatial allocation of the organic C and N pools and subsequent translocation towards zones of high metabolic activity (Lüning et al. 1973, Schmitz 1981). Beside *Laminaria* species, spatial and seasonal changes in thallus organic allocation have been described for highly differentiated species such as *Sargassum* (Prince & Daly 1981, Gorham & Lewey 1984), *Macrocystis* (Westermeier 1982, Wheeler & North 1981, Gerard 1982, Rosell & Srivastava 1985), *Lessonia* (Westermeier 1982, Percival 1983, Gómez & Westermeier 1995, Westermeier & Gómez 1996), *Durvillaea* (Westermeier 1982, 1987, Chesire & Hallam 1985, Lawrence 1986, Gómez & Westermeier 1995) and *Desmarestia* (Carlberg et al. 1978). Such characteristics certainly reflect adaptive mechanisms to withstand resource limitation in seasonal changing environments, which have finally led to the ecological success of these algae in different geographical regions (Lüning 1989).

Data on organic composition for Antarctic and cold-temperate brown algae reveal comparable values of total protein, mannitol and laminaran (**Table 10**). In general, proteins exceptionally exceed 20 % DW, with most of the values ranging between 5 and 15 % DW. However, these data should be interpreted with care because an important fraction of the variance between geographic regions and species may be accounted by differences in the extraction methods. For example, the relatively high protein contents close to 20 % DW reported for the Antarctic algae *Himantothallus grandifolius* and *Desmarestia menziesii* by Dhargalkar et al. (1987) may have to been caused by an over-estimation of proteins using the conversion factor 6.25 as this factor generally does not discriminate between protein and non-protein nitrogen such as ammonia, peptides, free amino-

Table 10 Protein and storage carbohydrates (% DW) in some large brown algae from Antarctic and cold-temperate geographical regions. Values represent maxima and minima reported in each study. Season when material was sampled is indicated in parenthesis. Wi = winter; Sp = spring; Su = summer; Au = autumn; Ann = annual average. Data correspond to middle lamina regions. [a] Values from Gagné et al. (1982) on a fresh weight basis.

Species	Location	Protein	Mannitol	Laminaran	Reference
Cold-temperate:					
Laminaria spp	Berufjördur (Iceland)		4 (Wi)-18 (Su)	6 (Wi)- 19 (Su)	Sjøtun & Gunnarson (1995)
Laminaria saccharina	Scotland	4.6 (late Su)-15 (late Wi)	4.5 (Wi)- 26 (Su)	absent (Wi)- 26.7 (Su)	Black (1948)
Laminaria longicruris	Nova Scotia (Canada)		< 1 (Su)- 5 (Wi)	< 1 (Su)- 7.5 (Au)	Chapman & Craigie (1978)
	Nova Scotia (Canada)		< 0.5 (Wi)- 5 (Su-Au)	< 0.5 (Wi)- 6-13 (Su)	Gagné et al. (1982)[a]
Macrocystis pyrifera	Laguna Beach (California)		6 - 33 Wi)		Gerard (1982)
	Valdivia (south Chile)	12.9 ± 1.7 (Su)	12.8 ± 0.6 (Su)		Gómez & Westermeier (1995)
	Valdivia (south Chile)	8.5 (Wi)- 13.4 (Sp)		0.7 (Su)- 3 (Su)	Westermeier (1982)
Saccorhiza polyschides	Port Erin (Isle of Man)	9.4 (Su)-13 (Sp)	2.5 (Au)- 11 (Su)		Jensen et al. (1985)
Sargassum pteropleurron	South Florida	10.5 (Wi)- 13 (late Au)	6.8 (Su)- 9 (Au)	1 (Su)- 5 (Au-Wi)	Prince & Daly (1981)
Postelsia palmaeformis	Pigeon Point (California)	6.4 ± 1.4 (Su)			Lawrence & McClintock (1988)
Durvillaea antarctica	Morbihan Bay (Kerguelen)	3.4 ± 1.7 (early Su)			Lawrence (1986)
	Valdivia (south Chile)	10 ± 2.8 (Su)	9.1± 0.5 (Su)		Gómez & Westermeier (1995)
Lessonia nigrescens	Valdivia (south Chile)	11.9 ± 1.7 (Su)	8.0 ± 0.5 (Su)		Gómez & Westermeier (1995)
	Valdivia (south Chile)	11 (Sp)- 25 (Su)			Westermeier & Gómez (1996)
Antarctic:					
Himantothallus grandifolius	King George Island	10.1 ± 1.3 (Su)			Czerpak et al. (1981)
	Signy Island		2.5 (Wi)-19 (Su)		Drew & Hastings (1992)
	King George Island	10.2 ± 2.5 (Su)	10.1 ± 0.4 (Su)		Gómez & Westermeier (1995)
	Vestfold Hill	19.6 ± 2.1 (Su)			Dhargalkar et al. (1987)
Ascoseira mirabilis	King George Island	9.1 ± 1.1 (Su)	9.7 ± 0.5 (Su)		Gómez & Westermeier (1995)
	King George Island	6 (Sp)- 13 (Sp-Su)	3.5 (Sp)- 13 (Su)	3.5 (Su)- 9 (Sp)	Gómez & Wiencke 1997b
Desmarestia menziesii	Vestfold Hill	20.6 ± 0.4 (Su)			Dhargalkar et al. (1987)
	King George Island	10 (Su)- 22 (Sp)	4-5 (Sp)- 8 (Su)	2.5 (Sp-Su)- 7 (early Sp)	Gómez et al. 1997b
Cystosphaera jacquinotii	King George Island	8.3 ± 1.9 (Su)	8.0 ± 0.5 (Su)		Gómez & Westermeier (1995)

or nitrates (Gnaiger & Bitterlich 1984, Rosell & Srivastava 1985, Aitken et al. 1991). On the other hand, similar protein values close to 10 % DW determined by Czerpak et al. (1981) and Gómez & Westermeier (1995) in *Himantothallus grandifolius* using also the factor 6.25 are significantly lower than those reported by Dhargalkar et al. (1987) suggesting seasonal or developmental effects.

Total proteins may vary following the seasonal changes in ambient N availability (Jensen et al. 1985) and therefore for cold-temperate species low protein contents in summer may be expected (Black 1948, 1950, Jensen et al. 1985). However, as observed in species such as *Sargassum pteropleuron* (Prince & Daly 1981) and *Lessonia nigrescens* (Westermeier & Gómez 1996), this is not a general pattern since several species can store N and thus synthesis of proteins becomes uncoupled from external N supply. In the case of Antarctic macroalgae, whose N metabolism is not ambient N limited, seasonal changes in proteins should be caused by other factors. In field plants of *Ascoseira mirabilis*, protein contents erratically vary between 5 and 13 % DW during the growth phase, apparently related to the total C and N levels (Gómez & Wiencke 1997b). In contrast, protein contents determined in *Desmarestia menzeisii* decrease gradually from 22 % DW in early spring to 10 % DW in summer being related to metabolic activity, increase in storage carbohydrates and water content in the thallus (Gómez et al. 1997b). In branched forms as in *D. menziesii*, expansion of the cellular volume during growth increases the photosynthetic area and could be accompanied by increases of other non-protein compounds, e.g. cell wall insoluble carbohydrates (alginic acid) and consequently decreasing the relative contribution of proteins to the total tissue weight. Degradation could also account for the decreases of proteins between spring and summer, but as amino acids did not markedly increase, it is reasonable to argue that proteins were totally degraded or cleaved to peptides.

Moreover, it is likely that high ambient N supply exceeds substantially the N requirements for protein and amino acid synthesis and free N is accumulated in surplus. In contrast, proteins appear to be the dominant N-compounds in

Ascoseira mirabilis, however, the significant direct relation between seasonal changes in amino acids and mannitol and the inverse relationship amino acids *vs* laminaran contents suggests strongly that amino acids are involved in remobilization of storage carbon as is the case in *Laminaria* species (Lüning et al. 1973, Küppers & Kremer 1978, Kremer 1980).

Similar as in cold-temperate kelps, mannitol and laminaran contents in Antarctic brown algae vary strongly with season (**Table 10**). In species such as *Laminaria saccharina*, mannnitol and laminaran vary from total absence in winter (4.5 and 0 % DW, respectively) to high values close to 26 % DW in summer (Black 1948). In other species such as *Sargassum pteropleuron*, seasonal changes may become less marked (7 to 9 % DW; Prince & Daly 1981). In the case of the Antarctic *Himantothallus grandifolius*, mannitol can vary between 2.5 in winter and 19 % DW in summer (Drew & Hastings 1992), agreeing with the summer average of 10 found by Gómez & Westermeier (1995). For *Ascoseira mirabilis* and *Desmarestia menziesii* measured seasonally, mannitol and laminaran contents have clearly lower ranges of seasonal variation rarely exceeding 10 % DW. However, it must be emphazised that these data constitute early spring-summer determinations and lower values might probably be expected during winter.

The implications of the seasonal changes in mannitol and laminaran on the physiological processes of Antarctic macroalgae can be interpreted in a similar way as in *Laminaria* species. Like species of *Laminaria*, Antarctic algae suffer a photosynthetic C deficit during the growth period, i. e. carbon losses due to anabolism and dark respiration exceed photosynthetic carbon fixation, which must be compensate by remobilization of storage carbohydrates (Gómez & Wiencke 1997b). As has been previously discussed, the seasonal carbon budget of *Himantothallus grandifolius*, *Ascoseira mirabilis* and *Desmarestia menziesii* does not appear to be affected by ambient nutrient limitation in summer as in *Laminaria* species. Therefore, light conditions, especially seasonal changes in daylengths, are presumably the major environmental component affecting variability of organic composition in these algae. Such a scenario seems to be

most probable as daylength-dependent variations of storage carbohydrates have been recently documented in culture plants of *Laminaria hyperborea* (Schaffelke 1995), a species exposed generally to a severe ambient N limitation in summer (Sjøtum et al. 1996). Whether utilization of storage carbohydrates to supply metabolic requirements in Antarctic brown algae is exclusively triggered by daylength, is up to now not clear. In populations of *Desmarestia menziesii* growing at 30 m depth, high respiration rates and low incident irradiances can account for a negative metabolic C balance in spring therefore a possible use of stored carbon may be the only mechanism allowing growth of plants at these depths (Gómez et al. 1997a). On the other hand, evidence of accumulation of laminaran in distal parts *Ascoseira mirabilis* and its possible remobilization as mannitol or amino acids towards the basal growing region (Gómez & Wiencke 1997b) add a morpho-functional component that is closely linked to the seasonal growth.

Undoubtedly, the data summarized here not only have given useful new insight into the eco-physiology of the Antarctic macroalgae, but have also risen a lot of new questions. In this sense, changes in storage carbohydrates under controlled conditions of light and nutrients and the use of specific tracer to monitor C and N flux along the lamina should provide conclusive data on these important aspects. Moreover, changes in organic compounds in response to herbivory may also put these physiological processes into an ecological perspective to understand better the role and functions of macroalgae in the whole community.

9. CONCLUSIONS

1. Biomass formation in the studied algae is seasonally determined and closely related to the photosynthetic performance. The use of seasonally fluctuating daylengths demonstrated that not only growth but also changes in photosynthetic metabolism can be simulated in culture. In the light of the results, it is possible to conclude that daylength is the major environmental factor affecting the seasonal physiological performance of Antarctic brown algae. It was also demonstrated that the "season anticipator" strategy of *Ascoseira mirabilis* and *Desmarestia menziesii* are based in the ability of their photosynthetic apparatus to make use of the available irradiance at increasing daylengths in late winter-spring.

2. The seasonal activity of the basally located meristem in *Ascoseira mirabilis* confers to this species its perennial characteristics and determines the allocation of biomass along the lamina. Therefore, intra-thallus differentiation in O_2-based photosynthesis and carbon fixation represents a morpho-functional adaptation that optimizes conversion of radiant energy to primary productivity.

3. The heteromorphic generations in *Desmarestia menziesii* show different photosynthetic characteristic. Small gametophytes and early stages of sporophytes have by virtue of their fine morphology, high content of pigments per weight unit, high photosynthetic efficiency and very low light requirements for photosynthesis, better suited to dim light conditions than adults sporophytes. This strategy ensures the completion of the life-cycle under seasonal changing light conditions

4. Low light requirements for growth and photosynthesis are developed to cope with Antarctic seasonality and in parallel constitute adaptations to expand depth zonation of macroalgae. No differences in net P_{max}, photosynthetic

efficiency (α) and pigments contents between algae growing at depths between 10 and 30 m, underline the absence of photoacclimation. This enables algae to grow over a broad range of prevailing light climates. However, shortenings in the daily period for which plants are exposed to saturation irradiances for photosynthesis (H_{sat}) and low carbon balance (daily P/R ratios) at depths $\geq$ 30 m negatively affect primary productivity.

5. In general, data on growth and photosynthetic rates of Antarctic macroalgae at 0 °C are comparable to those measured in species from temperate and cold-temperate regions. This clearly indicates a major physiological adaptation to the polar environment.

6. The variations in tissue composition (C and N contents) and major organic compounds (proteins, amino acids and storage carbohydrates) in *Ascoseira mirabilis* and *Desmarestia menziesii* were related to seasonal changes in photosynthesis. High rates of dark respiration lead to a C deficit during active growth in late winter-spring seem to be the major factor determining these changes. Considering the complex anatomical characteristics of these species, a possible remobilization of compounds such as mannitol and amino acids is postulated.

7. Finally, the results of the investigations summarized here constitute important advances in our knowledge on ecophysiological processes of Antarctic macroalgae. However, they also open a series of new questions to be addressed in future research. For example, the examination of key enzymes involved in specific mechanisms of photosynthesis, carbon metabolism and temperature tolerance will provide comprehensive information about the nature of adaptative mechanisms that allow these macroalgae to survive in polar environments. In addition, studies focusing on carbon and nitrogen budget as well as the interactions with other components of the benthic community are indispensable to accurately estimate primary productivity of

these algae and certainly will increase our understanding of role and ecological functions of macroalgae in the whole Antarctic littoral ecosystem.

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