Photoacclimation of phytoplankton in different biogeochemical provinces of the Southern Ocean and its significance for estimating primary production

Die Photoakklimatisierung von Phytoplankton in verschiedenen biogeochemischen Provinzen des Antarktischen Ozeans und ihre Bedeutung für die Abschätzung der Primärproduktion

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ABBREVIATIONS

$a[\lambda]$	absorption coefficient
$a_d[\lambda]$	detritus absorption coefficient
$a_\phi[\lambda]$	phytoplankton absorption coefficient
$a_\phi{}^*[\lambda]$	chlorophyll-specific absorption coefficient
$\bar{a}_\phi{}^*$	spectrally weighted absorption coefficient of phytoplankton for PAR
ACC	Antarctic Circumpolar Current
ADP	areal daily primary production
α^*	the maximum light utilisation coefficient
APF	Antarctic Polar Front
APFZ	Antarctic Polar Frontal Zone
ASO	Atlantic-Southern-Ocean-algorithm developed in our study
BASO	Atlantic-Southern-Ocean-algorithm at blooms developed in our study
B_s	chlorophyll *a* and phaeophytin *a* concentration at the surface
BWF	biological weighting function
$B(z)$	chlorophyll *a* and phaeophytin *a* concentration at depth (z)
CCSZ	the coastal and continental shelf zone
CFC	chlorofluorocarbons
chl *a*	chlorophyll *a* concentration
CO_2	carbon dioxide
CZCS	Coastal Zone Color Scanner
DU	Dobson Unit
E_a	downwelling irradiance in the air
$E_d[\lambda]$	downwelling irradiance at λ
$E_0[\lambda]$	downwelling irradiance at subsurface water at λ
E_k	light saturation parameter
$E_z[PAR]$	downwelling irradiance of PAR at depth z
E_k	light saturation parameter
Φ_m	maximum quantum yield
F_m	maximum yield of fluorescence in PSII
F_o	minimum yield of fluorescence in PSII
F_v/F_m	quantum yield of electron transport in PSII
GP	Global-Processing-algorithm by Gordon (1983)
HNLC-area	„High-Nutrient Low-Chlorophyll“ area

HPLC	high pressure liquid chromatography
IV	*in vitro*
JGOFS	Joint-Global-Ocean-Flux-Studies
$k_c[\lambda]$	chl *a* -specific vertical light attenuation coefficient at λ
$k_d[\lambda]$	vertical light attenuation coefficient at λ
$k_g[\lambda]$	vertical light attenuation coefficient due to non algal material at λ
$k_w[\lambda]$	vertical light attenuation coefficient due to water at λ
λ	wavelength
$L_u[\lambda]$	upwelling radiance at λ
$L_w[\lambda]$	radiance just above the surface measured by remote sensing at λ
MAAs	mycosporine-like-amino-acids
MIZ	marginal ice zone
O_3	ozone
PAR	photosynthetic active radiation from 400-700 nm
phaeo *a*	phaeophytin *a* concentration
P^*_m	maximum chl *a*-specific photosynthetic production rate
$P^*(z)$	chl *a*-specific photosynthetic production rateat dept (z)
PSII	photosystem II
P versus E	photosynthesis as a function of irradiance
R_i	reflectance data
RUBISCO	ribulose biphosphate carboxylase / oxygenase
SAF	Sub-antarctic Front
SeaWiFS	Sea-viewing-Wide-Field-of-view-Sensor
SIS	simulated *in situ*
SO	Southern-Ocean-algorithm by Mitchell and Holm-Hansen (1991)
STC	Sub-tropical Convergence
TOVS	Tiros Operational Vertical Sounder
UML	upper mixed layer
UV-A	ultraviolet-A radiation from 320-400 nm
UV-B	ultraviolet-B radiation from 280-320 nm
UVR	ultraviolet radiation from 280-400 nm
Z_{eu}	euphotic depth, as defined by the depth where underwater PAR has decreased to 1% of the coincident surface value
Z_{UML}	upper mixed layer depth

SUMMARY

The present thesis summarises the results from a series of publications where the production process of phytoplankton was studied in the Southern Ocean in order to assess its regional variability as defined by provinces and to provide basic data which can be used as bases for the estimation of productivity in the Southern Ocean. In Decembre to January 1995-96 during the German JGOFS cruise ANTXIII/2 various bioptical measurements, including the spectral composition of the underwater light field and phytoplankton absorption characteristics, and experiments on the relationship between photosynthesis and irradiance (P versus E curves) in the PAR and UV range were performed in the Atlantic sector of the Southern Ocean. These data were used to calculate primary production rates integrated over the water column for various stations; in addition, a diagnostic model was established to estimate synoptically the mesoscale distribution of primary production at the ambient region of the Antarctic Polar Front by using in addition to the P versus E relationships and absorbance characteristics obtained at certain points (stations) within the survey area, on-line chl *a* and underwater light data measured by sensors contained in a towed undulating vehicle. The composition of the phytoplankton communities was derived from HPLC data on pigment composition and from the distribution of the various size fractions on total chl *a*.

Phytoplankton composition and primary productivity in the study showed a regional distribution which was reflected in different biogeochemical provinces of the Southern Ocean: the Antarctic Polar Front (APF) with a diatom bloom and very high productivity (>1000 mg C m^{-2} d^{-1}), the interfrontal area between the APF and the marginal ice zone (MIZ) of the Antarctic Circumpolar Current (ACC) with scarce phytoplankton biomass, low primary productivity (<300 mg C m^{-2} d^{-1}), and the MIZ with a *Phaeocystis* bloom of large colonies and productivity values of 560 mg C m^{-2} d^{-1}. The observed phytoplankton blooms occured at sites of shallow upper mixed layers (UML; at least <50 m) and stratified water columns creating a light climate giving enough potential to result in high production and growth rates. Grazing by small-size-class zooplankton probably influenced size-fractionated distribution and species composition of phytoplankton within the two bloom sites. Only at the northern boundary of the APF silicate concentrations were nearly depleted and this fact probably limited phytoplankton (mainly diatom) growth. Low temperature and low iron availability might have

restricted growth of phytoplankton in the whole area, because the maximum biomass did not reach 2.5 mg chl *a* m^{-3}.

In addition, the thesis provides evidence that differences in biooptical characteristics coincide with the different biogeochemical provinces of the Southern Ocean, where the study was performed:

- Enhanced levels of UVR caused by stratospheric ozone depletion impaired primary production in the Southern Ocean more strongly outside of phytoplankton blooms than within. Within the phytoplankton blooms at the APF and the MIZ, dynamic photoinhibition as an photoprotective mechanism was governing the effect of UVR. Outside of the bloom, primary production decreased significantly and phytoplankton photosynthesis exhibited photodamage. Only inside both blooms shallow upper mixed layers (UMLs) caused an underwater light field, which induced MAA synthesis and repair mechanisms of PSII at a turnover rate sufficient to compensate negative effects of UVR. Although in all samples a significant amount of MAAs had been measured, outside the blooms efficient protection by MAAs would have been only achieved with an investment > 10% of the dry biomass due to the small size of the cells (diameter <20μm) which as a response to a single ecological factor this is regarded as waste of energy for the algal cell.
- Compared with other oceanic regions attenuation of light by non-algal material was low since in the Southern Ocean riverine input of terrestrially derived humic and dissolved material is very low. At a large scale the diffuse attenuation coefficient of underwater light, $k_d[\lambda]$, was correlated with changes of chl *a*. However, measurements of the spectral absorption by phytoplankton showed more subtle variations in the optical properties that are related to the phytoplankton population structure, which were missing in the bulk analyses to which the diffuse attenuation coefficient is subjected. Absorption by phytoplankton normalised to chl *a*, $a_\phi^*[\lambda]$, within the blooms was far lower than outside of the blooms, and decreased significantly below the upper mixed layer. The regional differences in absorption characteristics are due to differences in pigment composition and the package effect, which depends on phytoplankton cell size and photoacclimation in accordance to the UML.
- The comparison of *in situ* chl *a* to reflectance data of our survey, obtained from upwelling data measured *in situ*, showed that due to the low concentration of non algal material the global-processing-algorithm developed by Gordon et al. (1983) fails for

deriving chl *a* from remote sensing reflectance data in the Southern Ocean (mean difference 150% ± 84%); furthermore, the Southern-Ocean-algorithm developed by Mitchell and Holm-Hansen (1991a) fails too in calculating reasonable values of chl *a* (mean difference to *in situ* data 250% ± 150%) because the observed regional differences in $a_\phi*[\lambda]$ result in different relationships between chl *a* and reflectance. In future, algorithms for deriving pigment concentrations from remote sensing reflectance data, should be even specific for the various biogeochemical provinces. Using different algorithms for the different provinces improved estimates by 50%.

This study showed that averaging chlorophyll and light attenuation values over depth, irradiance over the day and not spectrally weighting α, the slope of the P versus E curve, introduces severe errors in the calculation of primary production rates (mean difference 30-50% ± 10-40%). Hence, the spatial discontinuity in biooptical characteristics, recognised for conversion of reflectance data into chl *a*, has also to be considered when extrapolating *in situ* observations relevant for the estimation of primary production in space and time, to match satellite data.

ZUSAMMENFASSUNG

In der vorliegenden Doktorarbeit wurde der Produktionsprozeß des Phytoplanktons im Antarktischen Ozean untersucht. Damit wurden regionale Unterschiede der Produktivität ermittelt und Informationen geliefert, die als Grundlage für die Abschätzung der Produktivität im Antarktischen Ozean benötigt werden. Im Dezember-Januar 1995/96 wurden während einer deutschen Forschungsreise im Rahmen des JGOFS Programms verschiedene biooptische Untersuchungen, u. a. die spektrale Zusammensetzung des Unterwasser- Strahlungsfeldes, das Absorptionsverhalten von Phytoplankton und die Beziehung zwischen Photosynthese und Strahlung (sog. PE-Kurven) im UV- und im PAR-Bereich, durchgeführt. Diesen Daten wurden für die Berechnung von über die Wassersäule integrierten Primärproduktionsraten an verschiedenen Stationen genutzt; darüberhinaus wurde ein diagnostisches Modell entwickelt, das die synoptische Schätzung der Verteilung der Primärproduktion in der Region der Antarktischen Polar Front (APF) im mittleren Maßstab veranschaulicht. Dafür wurden die an verschiedenen Punkten innerhalb des Untersuchungsgebietes bestimmten Absorptionscharakteristiken und PE-Beziehungen, sowie kontinuierlich gemessene Chlorophyll- und Unterwasserstrahlungsdaten verwendet. Diese wurden mit Hilfe des „Sea-Soar" gemessen, ein vom Schiff geschlepptes Gerät, das sich unter Wasser in Wellen auf und ab bewegt. Zusätzlich wurde die Zusammensetzung der Phytoplanktongemeinschaft durch Bestimmung der Pigmentzusammensetzung mit HPLC-Analyse und der Anteile der einzelnen Größenklassen an der Gesamtbiomasse charakterisiert.

In unseren Untersuchungen zeigte sich eine regionale Verschiedenheit von Phytoplanktonzusammensetzung und Primärproduktion, die den verschiedenen biogeochemischen Provinzen des Antarktischen Ozeans entsprach: Die APF mit einer Diatomeenblüte und sehr hoher Produktivität (>1000 mg C m^{-2} d^{-1}), der Bereich zwischen APF und Eisrandzone (MIZ) im Antarktischen Zirkumpolarstrom (ACC) mit sehr geringer Phytoplanktonbiomasse und niedrigen Primärproduktionsraten (>300 mg C m^{-2} d^{-1}), und die MIZ mit einer *Phaeocystis*-Blüte und Produktionswerten von 560 mg C m^{-2} d^{-1}. Die Verteilung der Phytoplanktonbiomasse und der -produktivität wurde von einem Komplex untereinander in Beziehung stehender Faktoren bestimmt und ist das

Ergebnis verschiedener Wachstums- und Verlustfaktoren. Die beobachteten Phytoplanktonblüten traten nur dort auf, wo die Durchmischungszone an der Oberfläche eher flach (<50 m) und die Wassersäule stratifiziert war. Unter diesen Bedingungen wird ein Lichtklima erzeugt, das hohe Produktions- und Wachstumsraten ermöglicht. Der vorwiegend von kleinem Zooplankton ausgeübte Fraßdruck prägte die Größenverteilung und Gruppen-zusammensetzung der Phytoplanktongemeinschaft innerhalb der beiden Blüteregionen. Nur an der nördlichen Grenze der APF war die Silikatkonzentration so niedrig, daß sie wahrscheinlich das Phytoplanktonwachstum (v.a. das der Diatomeen) begrenzte. Die generell tiefen Temperaturen und niedrigen Eisenkonzentrationen haben möglicherweise das Wachstum von Phytoplankton im gesamten Untersuchungsgebiet eingeschränkt, da die maximale Biomasse eine Chlorophyll-Konzentration von 2.5 mg chl *a* m^{-3} nicht erreichte.

Zusätzlich konnte in der vorliegenden Arbeit erstmalig gezeigt werden, daß auch die festgestellten Unterschiede in den biooptischen Eigenschaften eine regionale Verteilung zeigen, die mit den verschiedenen biogeochemischen Provinzen des Antarktischen Ozeans übereinstimmt:

- Erhöhte UV-Strahlung, die infolge des stratosphärischen Abbaus von Ozon entsteht, beeinträchtigte die Primärproduktion im Antarktischen Ozean stärker außerhalb der beiden Regionen mit Phytoplanktonblüte als innerhalb davon. In den Blüteregionen führte erhöhte UV-Strahlung dazu, daß die Photosynthese „dynamisch" inhibiert wurde, was als Schutzmechanismus eingestuft wird. In der Region ohne Phytoplanktonblüte sanken die Primärproduktionsraten signifikant ab und der Photosyntheseapparat wurde geschädigt. Nur in den Blüteregionen wurde durch die flache und relativ stabile obere Durchmischungszone ein Lichtklima erzeugt, welches die Synthese von UV absorbierenden Substanzen (sog. MAAs) und die Reparationsmechanismen mit Umsatzraten induzierte, die eine Kompensation der negativen Wirkungen der UV-Strahlung ermöglichten. In allen Proben waren nicht unerhebliche Mengen von MAAs gemessen worden. Trotzdem hätte außerhalb der Blüten wegen Dominanz von Phytoplanktonzellen kleiner Größe (über 70% mit einem Durchmesser <20μm) ein ausreichender Schutz durch MAAs nur mit Einsatz von mehr als 10% der Trockenbiomasse erzielt werden können. So ein Aufwand, um einem einzigen ökologischen Faktor zu begegnen, ist vom energetischen Standpunkt aus gesehen sehr kostspielig.

- Verglichen mit anderen ozeanischen Gebieten ist generell im Antarktischen Ozean die Lichtattenuation von photosynthetisch nicht aktivem Material niedrig, da hier der Eintrag von Huminstoffen und gelösten Substanzen aus terrestrischen Gebieten sehr gering ist. Der diffuse Attenuationskoeffizient von Licht unter Wasser, $k_d[\lambda]$, war mit Veränderungen von chl *a* im gesamten Untersuchungsgebiet korreliert. Durch Messungen der spektralen Phytoplanktonabsorption wurden feine Unterschiede in den optischen Eigenschaften aufgedeckt, die mit der Struktur der Phytoplanktongemeinschaft in Beziehung gebracht werden konnten und sonst in der „groben" Berechnung zur Bestimmung des $k_d[\lambda]$ fehlen. Die Phytoplanktonabsorption normiert auf chl *a*, $a_\phi{}^*[\lambda]$, war innerhalb der Blütenregionen sehr viel niedriger als außerhalb, und sank unterhalb der oberen Durchmischungszone noch deutlich ab. Die regionalen Unterschiede der Absorptionseigenschaften entstehen durch unterschiedliche Pigmentzusammensetzung und den „package effect"; der „package effect" ist abhängig von der Zellgröße und der Anpassung an die Lichtverhältnisse, die von der Tiefe der Duchmischungszone geprägt werden.
- Der Vergleich von *in situ* chl *a* - Daten zu Reflektionswerten, welche aus Messungen von *in situ* gemessenen Lichtdaten bestimmt wurden, zeigte, daß aufgrund der geringen Absorption von photosynthetisch nicht aktivem Material der Global-Processing-Algorithm von Gordon et al. (1983) nicht genutzt werden kann, um chl *a* aus mit Fernerkundung gewonnenen Reflektionsdaten im Antarktischen Ozean zu berechnen (mittlere Abweichung zu *in situ* chl *a* von 150% ± 84%); außerdem kann auch hier nicht der Southern-Ocean-Algorithm von Mitchell und Holm-Hansen (1991a) angewendet werden, da die gemessenen Unterschiede der $a_\phi{}^*[\lambda]$-Werte eine unterschiedliche Beziehung zwischen chl *a* und Reflektion implizieren (mittlere Abweichung zu *in situ* chl *a* von 250% ± 150%). In Zukunft müssen Algorithmen zur Bestimmung von Pigmentkonzentrationen aus Fernerkundungs-Reflektionsdaten entwickelt werden, welche spezifisch für die einzelnen biogeochemischen Regionen sind. Dies wird zusätzlich gerechtfertigt durch die Tatsache, daß durch die Benutzung unterschiedlicher Algorithmen innerhalb und außerhalb von Phytoplanktonblüten die Abschätzung von chl *a* im Mittel um 50% verbessert wird.

Die vorliegende Arbeit zeigt, daß bei der Berechnung von Primärproduktionsraten große Fehler durch folgende Vereinfachungen verursacht werden können: die Verwendung von Mittelwerten für Chlorophyllkonzentrationen und Lichtattenuationskoeffizienten über die euphotische Tiefe, sowie von Tageslichtmittelwerten und spektral nicht gewichteten α, dem Parameter, der die Steigung der PE-Kurve beschreibt. Wichtig für Schätzungen der räumlichen Verteilung der Primärproduktion wäre deshalb auch die *in situ* gemessenen Daten, zur Verwendung mit Fernerkundungsdaten in der Form zu extrapolieren, die die regionalen Unterschiede der biooptischen Eigenschaften berücksichtigt, wie es auch bei Berechnung von chl *a* aus Reflektionsdaten gemacht werden soll.

1. GENERAL INTRODUCTION

1.1 Marine primary production

Phototrophic primary producers are able to use solar energy for the build-up of their biomass using anorganic material. The biomass built up from anorganic substances over time is generally referred to as primary production, which is the basis for all other life on earth. Photosynthesis is the first step of primary production where solar energy is converted into chemical energy. Photosynthesis includes the absorption of photons by photosynthetic pigments and various photochemical reactions in which under the liberation of free oxygen adenosine diphosphate is converted to higher energy adenosine triphosphate (ATP), and nicotinamide adenine dinucleotide phosphate (or $NADPH_2$) is formed. These compounds are subsequently used for the fixation of inorganic carbon. In the second step of primary production, so-called biosynthesis, the end products of high energy carbohydrates (usually polysaccharides) and other organic compounds (including lipids, amino acids, and proteins) involving the uptake of anorganic nutrients are produced that comprise the cell (Kirk 1994a).

Phytoplankton are the dominant primary producers of the pelagial. Phytoplankton biomass in the oceans only amounts to 1-2 % of the total global plant carbon. Despite its relatively low biomass, these organisms collectively fix between 30 and 50 X 10^9 tons of carbon per annum by photosynthesis, i.e. is no less than 30-60% of the global annual fixation of carbon on Earth (Berger et al. 1989, Falkowski and Woodhead 1992, Falkowski 1995). Therefore, the functioning of the entire ecosystem of the world's oceans is dependent for energy almost on the photosynthetic activity of the small phytoplankton confined to the thin layer of lighted surface waters of the oceans.

The process of photosynthesis began to evolve in the ocean about 2000 million years ago (Callot 1991, Scheer 1991). Photosynthesis had a dramatic impact on the biogeochemistry of the earth, changing its environment from oxygen-poor, UV-rich and chemically-reducing environment to the oxygen-rich, geochemically more corrosive environment of the present day (Lovelock 1979, Walker et al. 1983). Classically, phytoplankton are recognised as the basis of most food webs upon which the world's fisheries are based. It is important to be able to monitor these phytoplankton populations since failures in the abundance and timing of algal blooms can lead to the collapse of fisheries.

The present biological productivity of the ocean is of central concern to a world concerned about global climate change. Indeed, phytoplankton can themselves influence the global chemical budgets and climate change by a number of mechanisms:

The utilisation of carbon dioxide through photosynthesis affects the global carbon cycle via the biological pump: Sedimentation of phytoplankton can result in a carbon transport from the atmosphere into deep ocean layers which are not in exchange with the atmosphere (Longhurst 1991, Lewis 1992, Sarmiento and Siegenthaler 1992). This is most effective during intense phytoplankton blooms, when a rapid build-up of biomass can greatly affect the carbonate system (Codispoti et al. 1982) which is typically seen in high sedimentation rates upon nutrient exhaustion (e.g. Smetacek 1985). To predict the response of the ocean (and the significance of the biological pump) to increasing amounts of the greenhouse gas carbon dioxide (CO_2) in the atmosphere is still difficult, due to uncertainities about relevant processes and rates determining carbon fluxes (Longhurst 1991).

In addition to that, the production of volatile compounds (e.g. dimethylsulfide (DMS)), derived from several major phytoplankton species, escape into the atmosphere and act as cloud seeding nuclei in the marine atmosphere (Charlson et al. 1987), and the absorption and backscattering of biogenic particles affect the albedo of the ocean and the rate of heating the surface water (Sathyendranath et al. 1991).

1.2 Southern Ocean

The Southern Ocean is defined by water masses marked by the northern boundary of either the Sub-tropical convergence (STC) or the Subantarctic Front (SAF). The STC is specified by the Joint-Global-Ocean-Flux-Studies (JGOFS) as the northern boundary of a coherent body of circumpolar Antarctic water, while the SAF forms a more natural biogeographic interface and is considered by Smith and Nelson (1986) and more recent studies (Priddle et al. 1996) as the northern boundary of the Antarctic Ocean. The total area of the Southern Ocean comprises 20% south of the SAF, 10.6% south of the

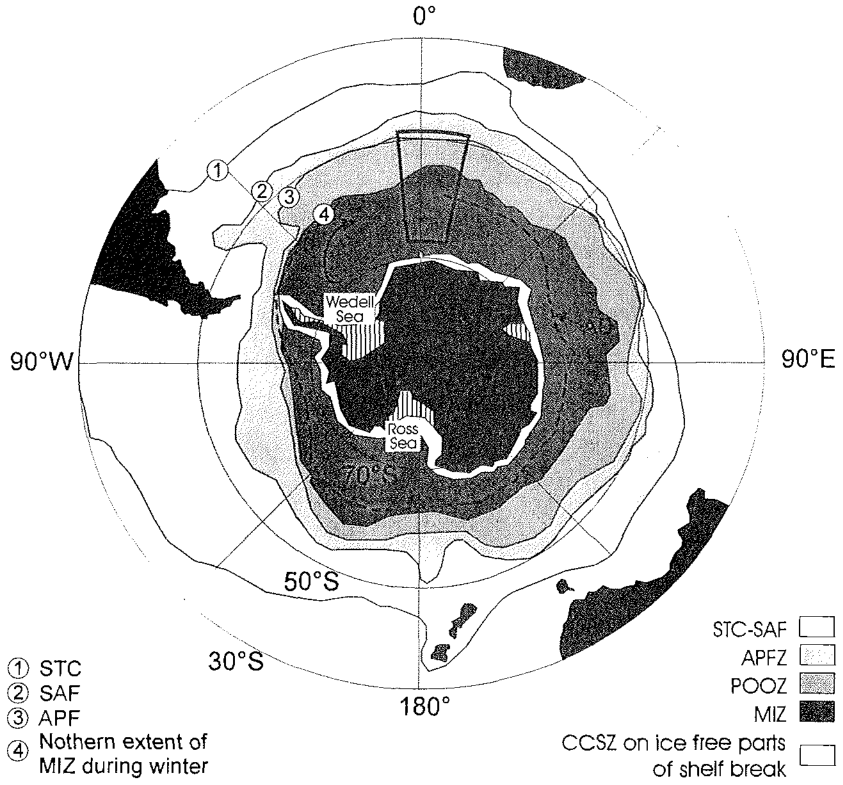

Fig. 1.1: Map of the Southern Ocean according to the description by Treguer and Jacques (1992). The Southern Ocean circumscribes the Antarctic continent and covers the southern areas of the Atlantic, Indian and Pacific Oceans. The northern border of the Southern Ocean is marked by the Subantarctic Front (SAF), but many studies refer to the Southern Ocean as to the water masses south of the zone of convergence at about 40°S (Sub-Tropical Convergence = STC). The main current is the Antarctic Circumpolar Current (ACC), which flows continuously around the Antarctic continent in a clockwise direction, driven by the prevailing westerly winds. The transition zone between the SAF and the Antarctic Polar Front (APF) is marked by the Antarctic Convergence, also referred to as the Antarctic Polar Frontal Zone (APFZ). The marginal ice zone (MIZ) of the Southern Ocean which varies in accordance to the season and is shown here in its maximal extension during winter. The zone between the APF and MIZ is described as the permanently open ocean zone (POOZ). South of the MIZ on the ice-free parts of the shelf is the coastal and continental shelf zone (CCSZ). The winds over the Antarctic mainland are predominantly easterly winds, driving the coastal current. The transition of the eastwards flowing ACC and the westwards flowing coastal currents is referred to as the Antarctic Divergence (AD). Here, part of the deep North Atlantic water, upwelling in the region of the ACC, comes to the surface. The local anomaly in surface temperature, however, is low and not easily discernible (from Sievers and Nowlin 1988, Orsi et al. 1995). The black frame marks the area where all studies in this thesis were performed

Antarctic Polar Front (APF) of the world's ocean (Fahrbach 1995). This thesis focuses on the area from the APF south to the marginal ice zone (MIZ) of the Southern Ocean (Fig. 1.1).

Until the early sixties, it was believed that the Southern Ocean was very rich in primary production based on the obvious assumption that the maintenance of the observed large animal stock required correspondingly high levels of the basic primary producers in Antarctic waters, the phytoplankton. In the seventies and eighties intensive research of the Southern Ocean was related to increasing interest in the exploitation of the krill as a major world food supply. During that time, the view of the Antarctic ecosystem was imprinted by a short food chain from large phytoplankton (diatoms) to krill. Since krill swarms are grazing intensely on phytoplankton, the studies involved measurements on phytoplankton biomass and production. Later on the plans on using krill as the world's major protein supply had been resigned, because it became clear, that in the Southern Ocean primary productivity is low in large parts (El-Sayed 1984), nanoplankton cells (<20 μm) may sometimes comprise more than 50% of the phytoplankton biomass (von Bröckel 1981, Koike et al. 1986) and more than 90% of the primary production (von Bröckel 1985), and the foodweb structure is much more complex, with the larger part occupied by food webs without much krill (Hempel 1985). Former estimates of krill stocks had to be corrected by an order of magnitude (Lubimova 1983).

Not only due to its volume, and thus potential for phytoplankton production, but also due to its hydrographic features the Southern Ocean is thought to play a critical role in the global climate system. Relatively rapid exchange of deep water masses with surface waters, and subsequently the atmosphere, make it an area that is extremely sensitive to fluctuations in atmospheric CO_2 (Siegenthaler and Sarmiento 1993). In the Southern Ocean, important sink areas for CO_2 are observed along the confluence zones (Antarctic Polar Frontal Zone, APFZ), where deep water formation of Antarctic Intermediate Water (AAIW) results in the transport of CO_2 into the deep ocean. On the other hand, the Antarctic Circumpolar Current (ACC), the main current that flows clockwise around the Antarctic continent, is an area where upwelling takes place on a large scale. As a consequence, the Southern Ocean would be a source of CO_2, via upwelling of water masses rich in CO_2 due to deep mineralisation of organic matter (Takahashi et al. 1993).

The incorporation of CO_2 in phytoplankton biomass may counterbalance or even exceed the CO_2 supply by upwelling. In the Southern Ocean grazing events have been observed where swarms of krill consume phytoplankton blooms within several hours (Jacques and Panouse 1991). The faecal pellets that are subsequently produced ensure considerable transport of carbon from the surface layers to the ocean floor, then biologically driven carbon transport can be considerable and result in an undersaturation of CO_2 in the surface waters (Wefer et al. 1988). Also at other sites of bloom formation in the Southern Ocean the undersaturation of CO_2 in the surface water was measured, which resulted in an uptake of CO_2 from the atmosphere (de Baar et al. 1995, Robertson and Watson 1995, Bakker et al. 1997). However, observations on nitrogen-isotope records preserved in Southern Ocean sediments, along with several geochemical tracers for the settling fluxes of biogenic matter, indicate that surface water stratification, rather than increased export production, was the primary process contributing to the lowering of atmospheric CO_2 during the last glacial period (Francois et al. 1997). It is yet unclear whether the net effect of these processes result in the Antarctic Ocean being a source or a sink for CO_2.

1.2.1 Primary production and the Antarctic Paradox

Today it is obvious that primary productivity in the Southern Ocean is spatially and temporally highly variable (Sullivan et al. 1993); however, compared to other regions maximum phytoplankton growth rates are generally low (<0.6 d^{-1}) due to low temperature (Sakshaug and Slagstad 1991). In spring and summer, phytoplankton blooms are frequently observed at coastal regions, near the ice-edge and at frontal zones systems; however, despite high levels of the major nutrients in the surface water, which are maintained by the combined effects of wind stress and thermohaline circulation which result in circumpolar surface divergence and upwelling (e.g. Bainbridge 1980, Nelson et al. 1987), the main body of the Antarctic Circumpolar Current (ACC) is characterised by low levels of biomass and primary productivity, <0.5 mg chl *a* m^{-3} and <300 mg C m^{-2} d^{-1}, respectively (e.g. Holm-Hansen et al. 1977, El-Sayed 1978, Sakshaug and Holm-Hansen 1984, Holm-Hansen and Mitchell 1991). Therefore, this region of the Southern Ocean like the subarctic Pacific and the equatorial Pacific, is called a „High Nutrient- Low Chlorophyll" (HNLC) area. In these areas phytoplankton do not exhaust phosphate and nitrate in the surface waters. This results in a "slippage" of the global coupling between the supply of nutrients to the surface and organic synthesis, and hence, a less efficient transfer of carbon from surface to deep waters via the biological pump (Chisholm and Morel 1991).

In a paper on Antarctic ecology, Hart (1934) discussed several potential reasons for the lack of nutrient utilisation including seasonal light, grazing, temperature, physical mixing, and iron limitation. Over the past decades, based on these concepts, oceanographers have put forward several hypothesis to explain the lack of phytoplankton blooms in the HNLC area, the so-called „Antarctic Paradox" (Treguer and Jacques 1986). Today, it is commonly accepted that the alternative hypotheses to explain the dynamics of the phytoplankton community are not mutually exclusive, and that different factors can be effective at different times and places (Cullen 1991, Lehmann 1991).

Patterns of phytoplankton biomass and primary production are determined by a complex interaction of growth and biomass-build-up:

Biomass build-up is discussed to be prevented through a tight coupling between microzooplankton and the flagellates, that constitute mainly the phytoplankton community in the Antarctic HNLC areas. The grazers have found to have equally high growth rates as their prey, and can therefore respond rapidly to any potential increase in phytoplankton biomass (Smetacek et al. 1990, Dubischar and Bathmann 1997, 1998). Also the episodic passages of krill swarms have been illustrated to be of importance in depleting diatom blooms in ice free planktonic communities (Smetacek et al. 1990, Lancelot et al. 1991)

Phytoplankton growth may be dictated by resource availability, such as light and temperature limitation, trace metal deficiency (iron), and physiological inefficiency. Any unfavourable growth condition would result in a retarded phytoplankton growth rates (rate limitation). Furthermore, extreme limitation of one of these factors would result in a complete blockage of phytoplankton growth (stock limitation). This could occur when the concentration of an essential element approaches zero, or when the light intensity is below the threshold for net growth. In the following, the different factors limiting the rate of phytoplankton growth are discussed.

Iron

Iron is an essential element for synthesis of several structural components used in photosynthesis and other processes within the cell (Geider and LaRoche 1994) and is considered the most necessary trace metal for algal growth (Scharek et al. 1997). Martin (1990) and Martin et al. (1990a, 1990b) claimed that iron fertilisation of the Southern Ocean would promote a phytoplankton bloom sufficient to remove from the atmosphere substantial amounts of the CO_2 derived from fossil fuel. Their hypothesis is based on two observations. First, the absolute concentrations of trace nutrients (i.e. iron) in open-ocean Antarctic waters are low relative to nitrate and other macronutrients (Martin et al. 1990b, de Baar et al. 1990) and second, experiments in which uncontaminated Antarctic near-surface waters were enclosed in bottles subjected to high light and additional iron resulted in rapid growth of some of the phytoplankton present and complete utilisation of the available macronutrients (i.e. nitrate) (de Baar et al. 1990, Martin et al. 1990a, Buma et al. 1991). Also ancillary observations support the iron hypothesis because they give evidence that the ACC has one of the lowest fluxes of atmospheric dust (Duce 1986) and that there is an inverse correlation over the last 100,000 years between aluminium dust (a proxy for iron and other trace elements in the atmospheric dust) and atmospheric CO_2 in Antarctic ice cores (de Angelis et al. 1987, Martin 1990).

Temperature

Water temperature in the Antarctic ranges from 5°C at the APF to -1.8°C in ice-covered waters towards the coast. These values are virtually constant and increase only slightly during the summer. The condition of permanently low temperatures imposes the first constraint on phytoplankton growth, since it slows down cellular processes such as the activity of enzymes. When light is saturating the photochemical apparatus of the cell a lowering of temperature will primarily lead to a decrease in photosynthesis (photosynthetic capacity; Neori and Holm-Hansen 1982). Under extremely low temperatures light-limited photosynthetic rates also become temperature dependent (Tilzer et al. 1986). Therefore, under low temperatures maximum specific growth rates of phytoplankton are reduced (Eppley 1972, Jacques 1983, Sommer 1989) and half-saturation constants for the uptake of silicate and nitrate are increased (Sommer 1986, Jacques 1983). Nevertheless, low temperature is not itself an explanation for the Antarctic Paradox, because maximum specific growth rates at *in situ* temperatures principally enable the development of a dense bloom within a few weeks (Jacques 1989).

Light conditions

Light is essential for receiving chemical energy by photosynthesis, therefore, phytoplankton growth depends above all on the availability of incident light, which is very variable in the Southern Ocean. The annual cycle of solar irradiance has a strong influence on phytoplankton growth (Smith and Sakshaug 1990). During late fall and winter, when light fluxes are low, productivity is marginal. During the summer months, the amount of light energy reaching the water column will depend on the sun or the transparency of the atmosphere. Near the Antarctic coast skies are often lightly clouded or clear. Here incident light fluxes may reach up to 2500 µmol photons m^{-2} s^{-1} on a summer day, and total daily fluxes exceed those of tropical latitudes. Photoinhibiton phenomena may occur frequently under this light conditions (*see* chapter 1.2.3 and 2.5). On the other hand over the open ocean low pressure systems develop continuously, which results in persistent cloud cover that attenuates 40-90% of the light (Bishop and Rossow 1991).

The amount of light penetrating the water column depends upon the absorption by suspended particles and the presence of ice. While the non-algal light absorption in the Southern Ocean is generally particularly low due to minimal terrestrial influx (Mitchell 1992), phytoplankton pigment concentration within the water column not only influences the light intensity, but also the spectral composition of the underwater light (Tilzer et al. 1994). Ice cover of the Southern Ocean varies highly over the year (5-25 Mio. km^2). Light is greatly attenuated by ice and in dependence of the snow cover, the ice may take away 15-99.9% of the irradiance that reaches the sea surface (Palmisano et al. 1987).

In addition to that, light conditions for phytoplankton photosynthesis also strongly depend on hydrological conditions: phytoplankton are the mercy of motions in the water column and therefore depend upon vertical mixing. Only during spring and summer phytoplankton blooms may develop mainly restricted to the areas of the marginal ice zone (e.g. Smith and Nelson 1985, Lancelot et al. 1993) and frontal systems (e.g. Laubscher et al. 1993, Jochem et al. 1995); here due to the stability of the water column the phytoplankton occur in the upper layers of the water column, where they can receive sufficient light for photosynthesis (Smith and Nelson 1986, Perissinotto et al. 1990). Records on wind speeds show that the wind stress driving the ACC is the largest of all oceans (Trenberth et al. 1990); this wind stress mixes in combination with relatively weak vertical stability the upper ocean and its resident assemblages over depth intervals (often >100 m), that result in a low time-integrated irradiance for the cells (e.g. Holm-Hansen et al. 1977, Smith and Nelson 1985). As a consequence, in the ACC, phytoplankton are subjected to highly variable light.

Although photoacclimation mechanisms allow the cells to maintain growth under very low light conditions and enable the cells to respond to rapid light fluctuations (*see* chapter 2.5), in large parts of the Southern Ocean, phytoplankton cells cannot maintain high growth rates; mixing induces a wind-mixed layer deeper than the critical depth as defined by Sverdrup (Sverdrup 1953, Nelson and Smith 1991). Sverdrup (1953) defined the „critical depth" as that depth at which the vertically integrated rates of photosynthesis and respiration by the phytoplankton were equal; blooming can only occur if the depth of the mixed layer is less than the critical value.

Mitchell et al. (1991) simulated Antarctic phytoplankton growth in a one dimensional ecosystem model including mixing depths, surface irradiance, grazing, sinking and respiration. The results of the model showed, that due to the persistent of mixed layers lower than 50 m in the ACC, which result in light deficiency, massive iron additions in the ACC would fail to significantly mitigate the atmospheric CO_2 derived from fossil fuel.

1.2.2 Ozone hole and ultraviolet radiation

In addition to greenhouse gases, changes in ozone (O_3) due to anthropogenic reasoning cause radiative forcing of the Earth's climate. Decreases in stratospheric ozone have occurred since the 1970s. There is mounting evidence that the solar flux of ultraviolet B radiation (UV-B) has increased at certain locations over the Earth's surface and this has been attributed to the continuing destruction of the ozone layer by atmospheric pollutants, in particular chlorofluorocarbons (CFCs) (Crutzen 1992). Since the stratospheric abundances of these compounds are expected to continue to increase for a few more years before they decline, stratospheric ozone losses are expected to peak near the end of the century, with a gradual recovery throughout the first half of the 21st century (Hougthon et al. 1996). Although these pollutants are mainly released from human activities in the Northern Hemisphere, the effects have been most clearly identified in the Antarctic region, where a unique combination of extreme cold and stratospheric circulation (the polar vortex) results in conditions that are favourable for the CFC-O_3 reactions (Anderson et al. 1991). Each year, the Antarctic „ozone hole“ (defined as a O_3-layer <200 Dobson Units (DU)) appears in spring. In October 1995 the average total O_3 values over Antarctica were 50-70% lower than those observed at the same time of the year in the 1960s (Houghton et al. 1996). While the depletion was first observed only in October, it has lately been present from September until December. Recently, significant ozone depletion has also been reported in the north polar region (Hofmann and Deshler 1991, Heese 1996).

Diminished stratospheric O_3 results in an increased flux of ultraviolet radiation (UVR), especially UV-B (280-320 nm), reaching the surface of the Southern Ocean and the upper part of the euphotic zone (i.e. 10% of surface UVR can penetrate to depths of 5 to 25 m; Smith and Baker 1981, Smith et al. 1992); effects on the UV-A (320 to 400 nm) and PAR (photosynthetically available radiation: 400-700 nm) portion are negligible (Smith et al. 1992, Stolarski et al. 1992). UV-B is known to have various deleterious effects on plants, including phytoplankton, especially with respect to growth and photosynthesis (e.g. Smith 1989, Rundel 1983, Caldwell et al. 1989, Coohill et al. 1989, Häder and Worrest 1991). Boucher and Prezelin (1996) determined the UV action spectra for Antarctic phytoplankton photosynthesis at a high spectral resolution. This study showed that phytoplankton are extremely sensitive to short wavelengths of UV-B and that this sensitivity decreases approximately exponentially as wavelength increases. By multiplying the wavelength-dependent UV action spectrum with the spectral irradiance, the effective action spectrum of UV (the so-called biological weighting function (BWF)) can be derived. Since with increasing ozone depletion the intensity of irradiance at shorter wavelegths is most strongly increasing, also the damage to photosynthesis by UV increases exponentially (Fig. 1.2). It was also shown that the BWF of UV inhibition of photosynthesis, varies with both the absolute amount of UV-B and the ratio of UV-B: UV-A+PAR, but not UVR: PAR (Cullen et al. 1992). Vertical mixing plays a crucial role in mitigating photoinhibition and UV-B exposure. Phytoplankton, as other marine organisms, employ a range of responses and adaptations to minimise their UV-B exposure. These include the synthesis of photoprotective pigments, DNA repair mechanisms, and avoidance mechanisms (Karentz 1994; chapter 2.5).

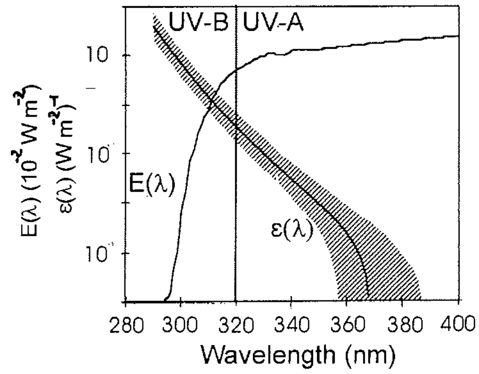

Fig. 1.2: Comparison of the daily averaged biological weighting function (BWF) for the *in situ* inhibition of primary production by UV radiation, ε(λ), and the average irradiance over the incubation time, E(λ), in Antarctic phytoplankton (from Boucher and Prezelin 1996)

Antarctic phytoplankton blooms reach their maximum biomass during late spring and early summer (November- January; Holm-Hansen and Vernet 1990), and it is reasonable to assume that phytoplankton blooms are initiated during the period of maximum ozone hole development. In addition to that, the Southern Ocean is considered most at risk from negative effects from increasing UV-B, because organisms are experiencing the greatest changes in UV-B here and have evolved under conditions relatively low in UV-B (Vincent and Roy 1993). Even under maximal development of the ozone hole, the flux of UV-B is still less than at low latitudes, rather it is the relative increase of UV-B to UV-A and visible radiation that is maximal in Antarctica. Effects of enhanced UVR during ozone depletion on Antarctic primary production may have an influence on the Earth's climate. Concern has been expressed that any diminution in marine primary production may lead to a positive feedback with respect to atmospheric CO_2, that would exacerbate the greenhouse effect (e.g. Smith et al. 1992). Also it has been found, that there are substantial differences between species in their response to UV-B exposure (e.g. Karentz et al. 1991a), indicating the possibility of shifts in community structure.

Such a shift would have consequences for both food web dynamics and biogeochemical cycles.

1.3 Methodological considerations

Reliable estimations of global marine primary production are difficult to obtain because of methodological problems and sampling limitations (Bidigare et al. 1992). Because of this, estimations of global daily primary productivity range from 50-2000 mg C m^{-2} d^{-1} (Bidigare et al. 1992). Since the Southern Ocean is an area remote from continents and its weather conditions are often characterised by heavy storms, shipboard measurements are especially difficult and expensive to conduct; therefore, the ocean cannot be sampled at all spatial and temporal scales, necessary to adequately resolve variations in phytoplankton biomass and productivity.

Particularly in this region, variations in chlorophyll *a* as revealed by satellite imagery, and validated by *in situ* measurements may improve estimations of marine primary production on the basis of the distribution of the phytoplankton biomass (e.g. Smith et al. 1982, Eppley et al. 1985, Platt and Sathyendranath 1988, Morel and Andre 1991, Behrenfeld and Falkowski 1997). No data on the net carbon fixation at a few given places are needed, but a set of the parameters of functions that relate the carbon fixation rate of phytoplankton to irradiance and chlorophyll, or light absorption (Sakshaug et al. 1997). The photophysiological responses of phytoplankton vary as a function of light regime, temperature and nutrient status. A major goal in understanding how phytoplankton photosynthesis affects carbon cycles, and is affected by ocean dynamics, is to determine how the photosynthetic processes respond to geochemical and physical processes.

Platt and Sathyendranth (1988) suggested that estimates of primary production at the global scale should be partitioned among biogeochemical provinces rather than being done within an ecological continuum. There are sufficient data of phytoplankton biomass for interpreting ocean colour data obtained by remote sensing on a global scale, but on the other side estimating primary productivity from remotely sensed information requires regional data on phytoplankton photosynthesis characteristics, which are, especially within the Southern Ocean, still much undersampled (Longhurst et al. 1995).

In addition to that, until now the remotely sensed signal can only be used to infer chlorophyll *a* concentration from measurements where light is reflected from near surface waters. Therefore, algorithms have been developed that combine ocean colour data with information on irradiance spectrum, phytoplankton biomass distribution within the vertical profile, and its photosynthetic characteristics in order to estimate areal integrated primary production (Platt and Sathyendranath 1988, Sathyendranath et al. 1989, Berthon and Morel 1992, Lewis 1992, Behrenfeld and Falkowski 1997). The advanced models differ from each other less in the philosophy of the approach than in the practical routes adopted for defining the distribution of parameters in time and space.

Mitchell and Holm-Hansen (1991a) demonstrated that using the global algorithm for deriving chlorophyll from ocean colour data developed by Gordon et al. (1983) gives a severe underestimation of phytoplankton chlorophyll concentrations in parts of the Southern Ocean. In addition, Mitchell (1992) demonstrated large differences in biooptical relationships for polar oceans as compared to temperate waters, and also between Antarctic and Arctic waters; the size of the data set and the multiple cruises for different regions implied that this conclusion is general. Therefore, it is of great importance to develop algorithms for deriving pigment concentration and estimating primary production which are specific for the Southern Ocean. In addition, the question if the same algorithm applies to the different hydrographic regions of the Southern Ocean has to be raised, since differences in optical properties of the underwater light spectrum in different regions of the Southern Ocean have been observed (Fenton et al. 1994, Stambler et al. 1997). Phytoplankton photoacclimation influences the properties of the underwater light field, by that consequently estimates of primary production from ocean colour data are affected.

1.4 Thesis outline

A principal topic of this thesis is the study of the production process of phytoplankton in the Atlantic sector of the Southern Ocean, mainly with the following objectives in mind:

- to assess the regional variability of the production process as defined by provinces within the Southern Ocean

- to investigate photoacclimation of phytoplankton to the underwater light field as an important strategy to maximise productivity and to minimise damage by excessive irradiance
- to specify effects of UV radiation on near-surface photosynthesis
- to provide ground-truth data which can be used for the estimation of productivity of the Southern Ocean over large areas from remote sensing information

Our knowledge of the productivity is important mainly for two reasons:

- to improve evaluations of the Southern Ocean's contribution to the global production process. This is of importance because the Southern Ocean comprises nearly 11% of the world's ocean and can be considered the largest upwelling region
- to provide information on the role of the Southern Ocean as a potential sink of atmospheric CO_2 by contributing to the removal of an important greenhouse gas

In Bracher and Tilzer (1999), regional characteristics of the spectral water transparency at the sample sites and the phytoplankton samples absorbance of visible light are shown. The regional characteristics of the underwater light field in this study are compared to results of other studies measured in the Southern Ocean. Differences in phytoplankton absorbance are interpreted as a result of different pigment composition (determined in Bracher et al. 1999) and pigment packaging, caused by the photoacclimational status and size of the phytoplankton cells (determined in Bracher et al. 1999). Data of this kind are of importance for modelling underwater light penetration and by that, for regional computations of primary production.

In Bracher et al. (1999), the distribution of primary production, biomass size fractions and photosynthetic pigment composition from HPLC-analysis of phytoplankton are determined. Photosynthetic characteristics of phytoplankton are studied by photosynthesis-versus-irradiance experiments. Biotic and abiotic factors influencing the regional distribution pattern of differences in primary production and the composition of the phytoplankton community are discussed. In addition, methodological aspects of determining daily primary production rates in the water column from *in vitro* incubations are discussed, focusing on the dependence of the responsible parameters on depth, time and the underwater light spectrum.

In Strass et al. (1999), a diagnostic model is established to estimate synoptically the mesoscale distribution of primary production at the Antarctic Polar Front. This three dimensional map of phytoplankton is developed by using on-line chlorophyll and underwater light data measured by sensors contained in a towed undulating vehicle, the so-called SeaSoar, and the photosynthesis-light relationships from *in vitro* incubations obtained only on certain points within the survey area. By intercalibrating the different radiation measurement systems, the spectral composition of light is considered. Distribution of primary production rates are compared to various abiotic parameters.

Both studies, Bracher et al. (1999) and Strass et al. (1999), give an insight on factors of controlling phytoplankton growth in the Southern Ocean. The results of these studies can be used for regional modelling of primary production resolved on a coarse and a fine spatial scale; this may include models of primary production where information on pigment concentration is derived from remote sensing data.

In Bracher and Wiencke (1999), the effect of sun spectra inside and outside the ozone hole on primary production rates and electron transport at photosystem II is considered. In addition, UV absorbing compounds in phytoplankton samples are determined. Phytoplankton damage by enhanced UV radiation and UV protection mechanisms at the different study sites are analysed. The observed substantial differences between phytoplankton communities in their response to UV-B exposure, indicate the possibility of shifts in community structure which may have consequences for both food web dynamics and biogeochemical cycles.

The main results of these studies are summarised here in a general discussion. The differences in phytoplankton photoacclimation shown in three biogeochemical provinces of the Southern Ocean (Bracher et al. 1999, Bracher and Tilzer 1999and Bracher and Wiencke 1999) and the methods used for obtaining areal primary production rates on a fine and a coarse scale (Bracher et al. 1999 and Strass et al. 1999) are evaluated in the context of the current debates on factors controlling phytoplankton growth and methods estimating primary production rates within the Southern Ocean, including models using ocean colour data obtained by remote sensing.

2. THEORETICAL ASPECTS OF MARINE PRIMARY PRODUCTION

This chapters focuses on various theoretical aspects of marine primary production which are relevant for the understanding of the biooptical studies performed in this thesis. This chapter includes a characterisation of the underwater light field, photosynthetic pigments, phytoplankton absorbance, the parameters describing the P versus E curve, photoacclimation and photoinhibition of photosynthesis.

2.1 Underwater radiation

During any day, the actual amount of radiation reaching the sea surface at any point is thus a function of the sun angle, the length of the day, and weather conditions. The intensity and quality of light reaching the pigments of the plankton algae depend on the optical properties of the water and on the incident light reaching the surface of the sea. Solar radiation coming to the outside of the Earth's atmosphere is fairly constant at about 1360 W m^{-2} (solar constant). About half of this energy is absorbed and scattered in the various layers of the atmosphere, so that the amount reaching the sea surface (referred as global radiation) is about 50% of that received at the top of the atmosphere. About 30% of the incoming solar irradiance is either reflected or scattered back into the outer space by the atmosphere and the Earth's surface. Some of this is reflected back into the atmosphere from the sea surface. The amount reflected from the sea surface depends on the sun angle and becomes very large below a sun angle of 5° to the horizon. This is influenced by the proportions of diffuse versus direct sunlight; if the diffuse part is high (e.g. under cloudy or hazy conditions) the dependence of the reflection on the sun angle is relatively small. The sun angle is determined by the time of year, time of day, and by the latitude. At the equator, the seasonal variation of daily irradiance is small, but, at 50°S, the seasonal variation in incident radiation ranges from about 140 kW m^{-2} d^{-1} in July to about 700 kW m^{-2} d^{-1} in December.

Only about 0.4% of the total solar radiation that reaches the Earth's surface belongs to UV-B (280-320 nm), while about 2% belong to the UV-A wavelength (320-400 nm), 46% belong to the photosynthetically active radiation (PAR, 400-700 nm) with wavelengths used by plants for photosynthesis and the remaining 50% belong to the infrared radiation (>700 nm). The maximum flux of energy of PAR with the sun overhead is about 400 W m^{-2}. This value also varies with the sun angle and decreases to zero as the sun approaches the horizon (Kirk 1994a).

In comparison with other liquids, pure water is relatively transparent to radiation with the exception to red light at wavelengths >600 nm, but much less than air. The infrared radiation is quickly absorbed and converted to heat in the upper few metres. The penetration of UV wavelengths into natural waters is highly dependent on the concentration of disssolved organic compounds and of particulate material; usually, it is rapidly scattered and absorbed within the water column (Kirk 1994b). However, in clear, ultraoligotrophic lake and ocean environments, the depth of 1% of surface radiation is 132 m for 360 nm and 30 m for 300 nm light, which was measured in a tundra lake by Smith and Baker (1981) and in the Southern Ocean by Smith et al. (1992). PAR is also scattered and absorbed in the water, with different wavelengths of the PAR spectrum penetrating to different depths. Red light (ca. 650 nm) is quickly absorbed, with only about 1% still remaining at 20 m in very clear seawater. Blue light (ca. 470 nm) penetrates deepest, with about 1% remaining at 100 m in clear water (e.g. Fig. 2.1 b, Fig. 2.2).

As a result of absorption and backscattering the downward irradiance, E_d, exponentially decreases with depth which is expressed by the attenuation coefficient of light, k_d. This attenuation coefficient can be calculated from measurements taken with a radiometer lowered into the sea, and using the following equation in which $E_0[\lambda]$ is the surface radiation and $E_d[\lambda](z)$ the radiation at depth z at a specific wavelength:

$$k_d[\lambda] = \ln (E_o[\lambda]/E_d[\lambda](z))/z \qquad \text{(equation 2.1)}$$

The amount of coloured dissolved organic material in seawater, and the amount of chlorophyll contained in living phytoplankton and in plant debris also affect the attenuation coefficient k_d. In very clear waters k_d is about 0.04 m^{-1} for blue light, and about 0.38 m^{-1} for red light (Bracher and Tilzer 1999). If many particles are present in the water, the blue light is scattered more than the red, and this will affect the colour spectrum of undersea light, resulting in a shift of the most deeply-penetrating wavelength toward a green colour (Fig. 2.1 a, c). At any given wavelength, vertical light attenuation in natural water bodies can be ascribed to the water itself (k_w), non-algal material suspended and/or dissolved in the water, (k_g), and phytoplankton. The

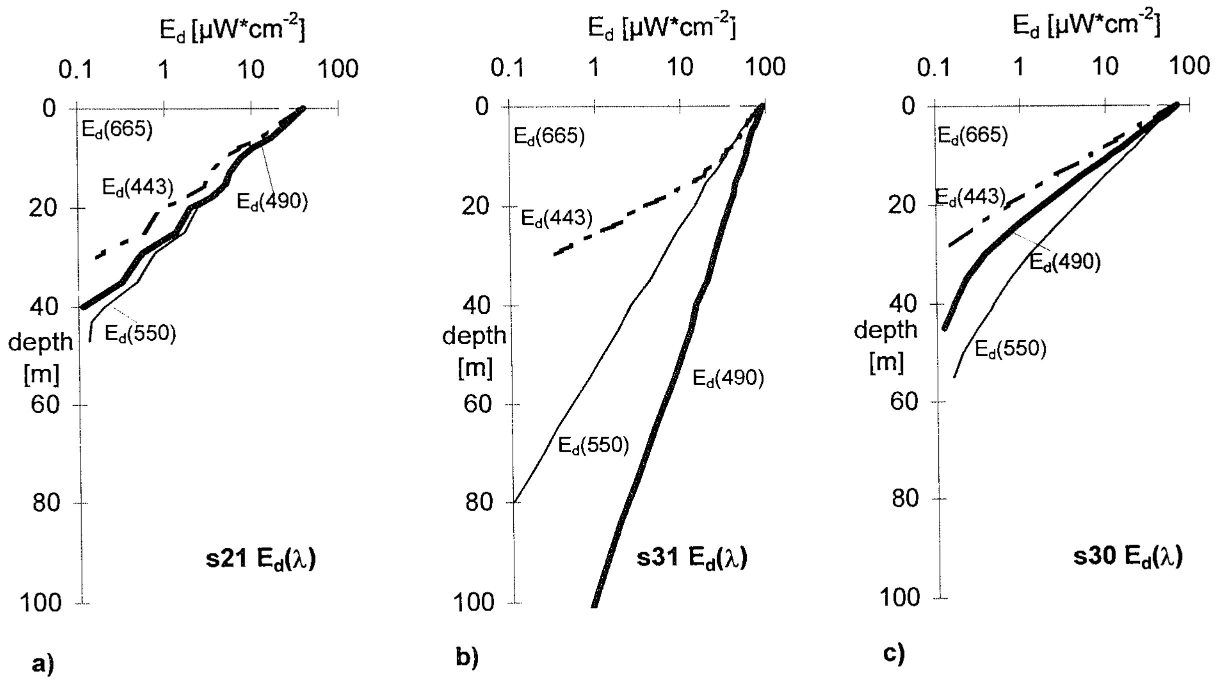

Fig. 2.1: Transmittance of downwelling irradiances (Ed[λ]) for 443 nm, 490 nm, 550 nm and 665 nm plotted semilogarithmically measured in the Southern Ocean during ANTXIII/2 cruise a) for Station S21 (a station within the APF), b) for Station S31 (a station within the ACC) and c) for Station S30 (a station within the MIZ). Figure was taken from Fig. 3 in Bracher and Tilzer (1999)

contribution of phytoplankton to overall light attenuation can be predicted by multiplying the chlorophyll-specific attenuation coefficient (k_c) by the respective chlorophyll (including phaeophytin) concentration, assuming that chlorophyll co-varies with the carotenoid pigments, all of which control light attenuation.

$$k_d[\lambda] = k_c \cdot [\text{chl } a + \text{phaeo } a] + k_w[\lambda] + k_g[\lambda] \qquad \text{(equation 2.2)}$$

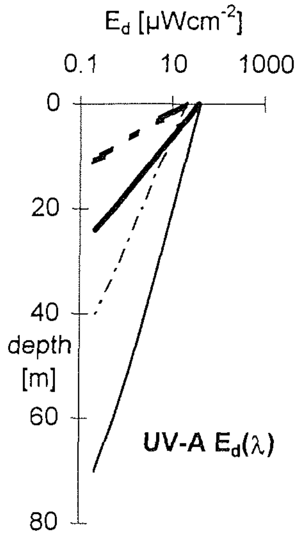

Fig. 2.2: Transmittance of downwelling irradiances ($E_d[\lambda]$) for 340 nm (broken lines) and 380 nm (solid lines) measured in the Southern Ocean during ANTXIII/2 at a station in the MIZ with high chl *a* (>2.0 μg l^{-1} at the surface; thick lines) and at a station in the ACC with low chl *a* (<0.5 μg l^{-1} at the surface; thick lines thin lines). Figure was taken from Fig. 6 in Bracher and Tilzer (1999)

2.2 Photosynthetic pigments

Light harvesting is carried out by the photosynhetic pigments. The three main pigment groups in photosynthetic phytoplankton are the chlorophylls, the carotenoids and the phycobiliproteins (Rowan 1989). In eukaryotic phytoplankton, these pigments are contained in the thylakoids in the chloroplast. The prokaryotic cyanobacteria do not have chloroplasts, but the pigments are nevertheless found in the thylakoids which are freely distributed within the cytoplasm (Kirk 1994a). All of these photosynthetically active pigments absorb light of wavelengths within the range of about 400-700 nm

(PAR), but each shows a different absorption spectrum. Often the accessory pigments, carotenoids and phycobiliproteins, dominate over the green colour of chlorophyll, and therefore many phytoplankton appear to be brown, golden, or even red in colour. Some pigments are species-specific and therefore can be used as taxonomical markers (*see* Bracher et al. 1999).

2.3 *In vivo* light absorption

The absorbance spectrum of a cell or colony suspension (in the case of unicellular algae) will be found to differ noticeably from that of dispersed thylakoid fragments. The *in vivo* light absorption characteristics of phytoplankton depend mainly on the pigment composition of the cell and the package effect (Johnsen 1994). The package effect is defined as the reduction of the light absorption of a suspension of pigmented particles (living phytoplankton cells) relative to the same amounts of pigments in solution (dispersed thylakoid fragments, "unpacked absorption", cf. Kirk 1994a). It is a consequence of the fact that the pigment molecules, instead of being uniformly distributed, are contained in discrete packages: within chloroplasts, cells, and colonies. The package effect depends on a) pigment composition, b) cell size, shape or morphology, c) chloroplast size, shape, number, morphology and distribution, d) the degree of stacking of the thylakoid membranes, e) the optical properties of the thylakoid membranes and f) the orientation of the chlorphyll-containing body towards the incoming photons (Berner et al. 1989, Johnsen and Sakshaug 1993, Johnsen et al. 1994). The total particular absorption coefficient ($a[\lambda]$, m^{-1}) is corrected for detrital absorption ($a_d[\lambda]$, m^{-1}) to derive the absorption coefficient of phytoplankton ($a_\phi[\lambda]$, m^{-1}) by various methods (e.g. Kishino et al. 1985, Bricaud and Stramski 1991, Roessler et al. 1992, Cleveland and Weidemann 1993). It is a common practice to express $a_\phi[\lambda]$ as a specific absorption coefficent, $a_\phi^*[\lambda]$, and [chl *a* + phaeo *a*]:

$$a_\phi[\lambda] = a_\phi^*[\lambda] \cdot [\text{chl } a + \text{phaeo } a] \qquad \text{(equation 2.3)}$$

Changes in the absorption properties of phytoplankton, consequently affect the attenuation coefficient of phytoplankton $k_c[\lambda]$, since the latter depends on $a_\phi^*[\lambda]$. While $a_\phi^*[\lambda]$ only defines the specific absorption coefficient of phytoplankton which was determined by measurements of the beam attenuation in the laboratory with a spectrophotometer, $k_c[\lambda]$ includes scattering and absorption from irradiance coming from all directions since it is determined by linear regression of $k_d[\lambda]$ versus [chl *a* + phaeo *a*]. The difference between the values of $a_\phi{}^*[\lambda]$ and $k_c[\lambda]$ is due to geometrical differences of the irradiance during the two measurement techniques, which are mainly determined by scattering and the angle of the incoming irradiance (Kirk 1994a).

A useful concept when considering light capture by phytoplankton is the effective absorption coefficient of the phytoplankton population existing at a given depth for the light field at that depth, over the whole photosynthetic spectrum (PAR). This spectrally weighted absorption coefficient of phytoplankton for PAR, $\bar{a}^*$, is defined according to Atlas and Bannister (1980) by

$$\bar{a}_\phi{}^* = \frac{\sum_{700}^{400} a_\phi[\lambda]\, E_d[\lambda]\, \Delta\lambda}{\sum_{700}^{400} E_d[\lambda]\, \Delta\lambda} \qquad \text{(equation 2.4)}$$

2.4 Photosynthetic responses: The P versus E curve

The photon fluence rate strongly affects both the amount and rate of photosynthesis. The instantaneous rate of photosynthesis, P* [mg C (mg chl $a)^{-1}h^{-1}$], in a phytoplankton cell depends on the rate of capture of quanta of visible light (400-700 nm). The asterisk (*) in P* denotes that the photosynthetic rate (carbon uptake per unit of time) is scaled to chl *a* (Sakshaug et al. 1997). The light-capture rate is determined by the light absorption characteristics of the cell, the irradiance and its spectral composition (Morel et al. 1987, Johnsen 1994, Kirk 1994a). The gross photosynthetic rate increases linearly with irradiance and approaches the maximum photosynthetic rate, P^*_m (same units as P*). With further increase in irradiance, P* begins to decrease again, a phenomenon referred to as photoinhibition (*see* chapter 2.5). Figure 2.3 shows a typical photosynthesis versus irradiance (P versus E) curve which is determined by two parameters: the maximum light utilisation coefficient , α^*, [mg C (mg chl $a)^{-1}h^{-1}$ (µmol quanta $m^{-2}s^{-1})^{-1}$] which is the slope of the curve at the light-limited portion and a measure of photon capture and utilisation, and the maximum photosynthetic rate or photosynthetic capacity, P^*_m, [mg C (mg chl $a)^{-1}h^{-1}$]. A third parameter, the irradiance at onset of light saturation, E_k [µmol quanta $m^{-2}s^{-1}$], equals P^*_m / α^*. E_k indicates the irradiance at which control of photosynthesis passes from light absorption and photochemical energy conversion to reductant utilisation and may be a convenient indicator of photoacclimation and photoadaptation. The photosynthetic parameters are affected by the nutrient supply (including CO_2), temperature and salinity (Falkowski 1981, Morris 1980, Tilzer et al. 1993). The ability of aquatic plants, including phytoplankton, to utilise light of any given intensity can be highly dependent on the light climate to which they were exposed during growth; for ecological interpretation it is therefore preferable to measure P versus E curves on naturally occurring, rather than laboratory grown, plant material (Sakshaug et al.1997).

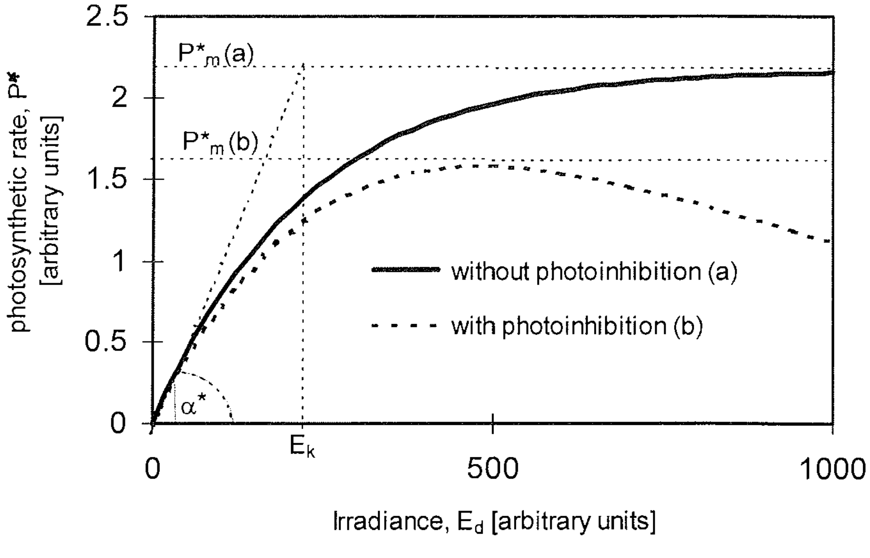

Fig. 2.3: Two typical photosynthesis versus irradiance (P versus E) curves (a) according to the equation 2.6 by Webb et al. (1974): $P^* = P^*_m (1-\exp((E\ \alpha^*)/ P^*_m))$, where α^* [mg C (mg chl *a*)$^{-1}$h^{-1} (μmol quanta $m^{-2}s^{-1})^{-1}$] is the slope of the curve at the origin and P^*_m, [mg C (mg chl *a*)$^{-1}$h^{-1}] is the maximum photosynthetic rate or photosynthetic capacity and (b) according to the equation 2.8 Platt et al. (1980) including inhibition: $P^* = P^*_m [1-\exp((-E'\ \alpha^*)/ P^*_m)] (\exp((-E'\ \beta^*)/ P^*_m))$, where β^* is the parameter chosen to characterise photoinhibition

The maximum light utilisation coefficient, α^*, is a spectrally dependent parameter and has to be corrected when the experimental light conditions differ qualitatively from the ones *in situ*, according to the relationship (Lewis et al. 1985):

$$\alpha^*_{\text{(spectrally corrected)}} = (\alpha^*_{\text{incubator}} \cdot \bar{a}_\phi{}^*_{\textit{in situ}}) / \bar{a}_\phi{}^*_{\text{incubator}} \qquad \text{(equation 2.5)}$$

Knowledge of P versus E parameters and their variability is crucial for modelling primary production on larger scales on the basis of monitored remotely sensed optical data (Smith et al. 1987, 1989, Prezelin an Glover al. 1991, Bidigare et al. 1992, Prezelin et al. 1992). A number of attempts have been made to find mathematical expressions which give a reasonable fit to the empirical curves relating P* to E. Here the description originally proposed by Webb et al. (1974) is chosen which excludes photoinhibition (since we did not find photoinhibition in our P versus E experiments performed in a photosynthetron - *see* Bracher et al. 1999).

$$P^* = P^*_m\,(1\text{-}\exp((E\,\alpha^*)/\,P^*_m)) \qquad \text{(equation 2.6)}$$

The quantum yield of photosynthesis, Φ, is defined to be the number of CO_2 molecules fixed or oxygen evolved in a biomass per quantum light absorbed by the plant. Morel (1978) calculated Φ at a series of depths from $^{14}CO_2$ fixation, chlorophyll and light data for a variety of oceanic waters. In most cases Φ increased with depth. Within the initial, linear portion of the P versus E curve Φ is constant and has its highest value (Bannister 1974). Therefore, the maximum quantum yield of photosynthesis, Φ_m, can be calculated from the equation (Bannister 1974):

$$\Phi_m = \alpha^*_{\text{(spectrally corrrected)}} / \bar{a}_\phi{}^*_{\textit{in situ}} \qquad \text{(equation 2.7)}$$

The maximum quantum yield represents the efficiency with which the photosynthetic apparatus converts absorbed photons to chemical energy. By calculating Φ_m from the phytoplanktonic component of absorption, changes in Φ_m can be related to phytoplankton physiology (Cleveland et al. 1989). In principle, Φ_m is spectrally dependent, in practice, however, it is usually treated as a non-spectral parameter (Sakshaug et al. 1997). Because studies of $\alpha^*(\lambda)$ are few, there are few accurate spectral estimates of $\Phi_m(\lambda)$ of photosynthesis in natural phytoplankton communities (Lewis et al. 1985, Schofield et al. 1993, 1996, Carder et al. 1995). It is generally accepted that Φ_m is 0.125 mol O_2 (mol photons)$^{-1}$, indicating that 8 quanta are required to produce one O_2 molecule (Kok 1960). For reasons not well understood, Φ_m for carbon fixation of phytoplankton populations in the oceans is extremely variable. Some of this spatial variation may have a genetic base, i.e. it may be due to the presence of taxonomically different phytoplankton populations: diatom-dominated communities in the Southern California Bight had Φ_m values twice as high as the cyanobacterial picoplankton in the deep chlorophyll maximum (Schofield et al. 1991). Some of it may have a physiological basis, due to populations differing in respiration rates (Lizotte and Priscu 1994), nutritional status (Cleveland et al. 1989), or recent light exposure history (Prezelin et al. 1991, Tilzer 1984). Reduction of nitrate to ammonium competes with CO_2 fixation for photochemically produced reductant, so that Φ_m for carbon fixation is lower than Φ_m for oxygen evolution when phytoplankton are grown on nitrate. As a consequence, the ratio of O_2 evolved to CO_2 fixed varies with the redox state of the nitrogen source (Megard et al. 1979). Bannister and Weidemann (1984) state a maximum for $\Phi_{m\ \textit{in-situ}}$ at 0.08 and claim that values >0.1 are almost certainly due to imprecision or systematic error.

2.5 Photoacclimation and photoinhibition

Compared to photosynthesis in a terrestrial milieu, photosynthesis in an aquatic environment differs in regards of the availability of light. Phytoplankton have to compete for light quanta with their surroundings due to the high optical density of water compared to air. Unlike in terrestrial environments, phototrophs can only utilise the absorption peak for blue light because even in very clear waters red light is absorbed quickly. Harvesting of underwater light by the photosynthetic antenna pigment is a function of pigment concentration and composition on the one, the spectral properties and the extent of light attenuation by the non-algal material on the other hand. Many phytoplankton species exhibit a remarkable physiological plasticity and are able to respond to wide variations in the light regime (irradiance, its spectral composition and daylength). The physiological acclimation of the photosynthetic apparatus to specific light conditions appear to have common molecular biological causes that are signaled by the redox status of specific elements in the photosynthetic electron transport chain (Escoubas et al. 1995). Acclimation to different light levels of irradiance is achieved by altering the cellular pigment contents. Falkowski et al. (1981) have demonstrated that there are two principle mechanisms: variation in the numbers or variations in the size of photosynthetic units. Both mechanisms are reflected in the alteration of the P versus E curve in response to variations in the ambient light field to which they acclimate. In addition to that, changes in the intensity and the spectrum of light are generally characterised changes in cell volume, the enzymatic activities involved in photosynthesis and respiration, chemical composition and respiration rate. In fluctuating light, photoacclimational responses apparently lower variations in the growth rate (Sakshaug and Holm-Hansen 1986). Photoacclimation is thus the sum of compensation mechanisms which allows the phytoplankton to grow under a wide range of irradiances at nearly the same optimum growth rate (the optimum range). The compensation is, however, not total. As the growth irradiance decreases, the growth rate will also be reduced, but the reduction is not as great as it would have been without photoacclimation.

When on a summer day, cells in the shallow upper layers of the sea are for extended periods exposed to high irradiance levels, photodamage of the photosystems can occur. In addition, UV damage due to ozone depletion may occur in the upper part of the water column. Equations that account for this high irradiance inhibition of photosynthesis have been developed by several investigators. Platt et al. (1980) extended the exponential formulation of Webb et al. (1974) (equation 2.6) to account for photoinhibition (Fig. 2.3):

$$P^* = P^*_m\,[1-\exp((-E\cdot\alpha^*)/P^*_m)]\,(\exp((-E\cdot\beta^*)/P^*_m)) \qquad \text{(equation 2.8)}$$

where β^* is the parameter chosen to characterise photoinhibition.

In order to quantify the biological effects of changes due to photoinhibition, wavelength-dependent weighting functions are required (Caldwell et al. 1989, Coohill 1989). Jones and Kok (1966) measured action spectra of photoinhibition of electron transport in spinach chloroplasts. The spectrum showed its main activity in the ultraviolet (UV) region with a peak at 250-260 nm. Photoinhibition also occurred in the visible region but with a very much lower quantum efficiency. Between 400 and 700 nm, the action spectrum followed the absorption spectrum of chloroplast pigments, with a distinct chlorophyll peak at 670-680 nm. Now, also among phytoplankton it has been found that the lesion appears primarily to affect the light reactions of photosynthesis, by damaging the reaction centre of photosystem II (PSII) and the carboxylating enzyme (RUBISCO)- e.g. Lesser et al. 1996. The shape of the action spectrum in the UV region suggests that plastoquinone or some other quinone functional in the reaction centre may be the sensitive molecule so far as UV inhibition is concerned. Biological and physical reactions with UV-B radiation increase sharply as wavelength decreases; the most damaging wavelengths are also the most difficult to measure (Kirk et al. 1994b). The shape of the action spectrum in the visible region indicates that at very high light intensities some of the energy absorbed by the photosynthetic pigments themselves is transferred to a sensitive site - not necessarily the same site as that affected by UV- where it causes damage. Choice of the biological weighting function (BWF) can have an overriding influence on the prediction of relative biological effects (Rundel 1983, Booth and Madronich 1994, Coohill 1994). While BWF have been described for temperate phytoplanktonic organisms (Cullen et al. 1992), Boucher and Prezelin (1996) determined a daily integrated *in situ* BWF for inhibition of primary production by UVR on a natural community of Antarctic diatoms under day light conditions. The BWF determined by Boucher and Prezelin (1996) displayed a greater sensitivity to UV-B than BWFs determined under laboratory conditions. Here daily exposure to ambient levels of UV resulted in a 34% reduction in average carbon fixation, while the O_3-dependent UV-B portion of the solar spectrum photoinhibited 15%, the O_3-independent UV-A portion inhibited 19%.

The sensitivity of phytoplankton photosynthesis to irradiance stress has been demonstrated by several studies, e.g. Neale (1987), Smith et al. (1992), Long et al. (1994). However, showing whether this stress actually occurs remains difficult. The essential problem is that phytoplankton cells are suspended in the water. Their irradiance exposure will be determined by mixing processes that transport the cells over a vertical gradient in light availability. Depth profiles of phytoplankton photosynthesis determined by the suspended bottle method, tend to overestimate the extent to which photoinhibition diminishes primary production since in such experiments phytoplankton are incubated under a constant light regime (Harris and Piccinin 1977, Marra et al.

1978). In nature the phytoplankton are not forced to remain at the same depth for prolonged periods. Since photoinhibition is usually a time-dependent process, the light history of the cells must be known to specify the overall effect. Although it is possible to deduce the rate of mixing from the light history of the phytoplankton (e.g. Falkowski 1983), the effect of photoinhibition cannot be simply calculated from the product of irradiance and duration of exposure. For instance, Cullen and Lesser (1991) have demonstrated that for equal doses of UV-B, short exposures to high irradiance are more damaging than longer exposures to lower irradiance.

Some measurements have tried to simulate mixing (Marra et al. 1978, Helbling et al. 1994); neither of these approaches allow an accurate estimation of photoinhibition in the water column. Neale et al. (1998) developed a model of UV-influenced photosynthesis during vertical mixing, where the potential effects of ozone depletion on daily photosynthesis integrated through the water column (areal daily primary production rate = ADP) were calculated. Inhibition of ADP could be enhanced or decreased by vertical mixing, depending on the depth of the mixed layer and on the mixing rate. Under all modelled conditions, photosynthesis was strongly inhibited by near-surface UVR and when mixing was rapid.

3. SUMMARY OF RESULTS

In this thesis different biological parameters determining primary production were studied in one part of the Atlantic Sector of the Southern Ocean (Fig. 1.1). All studies were performed during the German JGOFS-cruise ANTXIII/2 at the same time, December 1995 to January 1996, and the same phytoplankton samples were used for all studies. All phytoplankton samples were from the open sea. The study area of Bracher and Tilzer (1999), Bracher et al. (1999) and Bracher and Wiencke (1999) comprised an area between 49° and 67°S and between 6°W and 12°E, including the regions of the Marginal Ice Zone (MIZ), the Antarctic Circumpolar Current (ACC) outside of frontal systems and the Antarctic Polar Front (APF); the study area of Strass et al. (1999) was the area within and surrounding the APF, centred at roughly 50°S and 10°E (Fig. 1.1). While in Bracher and Tilzer (1999), Bracher et al. (1999) and Bracher and Wiencke (1999) biooptical characteristics were studied at stations, a three dimensional map of primary production was developed in Strass et al. (1999) by using on-line data of light and fluorescence obtained by a towed undulating vehicle. The results from all four publications characterised the three biogeochemical provinces, MIZ, ACC and APF, in the following way (*see* Table 3.1):

The Marginal Ice Zone

In the MIZ close to the ice edge a "second period bloom" (>2.4 mg chl *a* m^{-3}) was found within a water column of a shallow upper mixed layer (<15m). *Phaeocystis* was dominating the phytoplankton bloom with large colonies (over 60% >20 µm) (Bracher et al. 1999).

Within the euphotic zone, below the sea surface and within the shallow upper mixed layer, about 65% in the blue spectral range of the attenuated light were absorbed by phytoplankton; absorption was highest where phytoplankton biomass was highest. In contrast, specific absorption of phytoplankton, a_ϕ*, was low and significantly lower at depths below the upper mixed layer (Bracher and Tilzer 1999). P^*_m at surface were higher then at 1% light depth and primary production rates were high 560 C m^{-2} d^{-1} (Bracher et al. 1999).

Maximum primary production rates were not significantly influenced by enhanced UVR corresponding to conditions inside the ozone hole. The amount of UV absorbing compounds, mycosporine-like-amino-acids (MAAs), was rather low, but in combination with the on average prevailing big size of *Phaeocystis* colonies within the bloom, the sunscreen effect of those compounds may be big enough in addition with other UV protection processes to compensate inhibition by UV enhanced radiation (Bracher and Wiencke 1999).

Antarctic Circumpolar Current outside of frontal systems

This region was characterised by deep UMLs, which always exceeded 40 m and indicated low stability. From south to north salinity decreased and surface temperature increased, 34.50 to 33.86 and -1.5 to <4 °C, respectively. Biomass was low with values <0.5 mg chl *a* m^{-3} and maxima of chl *a* were found in 40 to 80 m. Dinophyceae, Prymnesiophyceae, diatoms and Cryptophyceae contributed equally to the phytoplankton community, and only 10 % of those phytoplankters were found to be bigger than 20 µm. (Bracher et al. 1999).

Within the euphotic zone only about 25% in the blue spectral range of light being attenuated were absorbed by phytoplankton. The contribution of phytoplankton on the total attenuation of light was increasing with increasing depth, which can be explained by the combination of strong red attenuation by water molecules already at the surface and low biomass. Specific absorption of phytoplankton, a_ϕ^*, was high due to the small cell size and did not change with depth because of deep UMLs (Bracher and Tilzer 1999). Primary production rates were low (110-300 mg C m^{-2} d^{-1}). However, in the south of the ACC at areas which were close to the ice edge, primary production rates were found to be 390 to 480 mg C m^{-2} d^{-1}. Here, more diatoms were found within the community (up to 40%) and chlorophyll maxima were at a shallower depth (20-40 m) (Bracher et al. 1999).

Maximum primary production rates were found to be significantly decreased by UVR corresponding to conditions inside the ozone hole. An explanation for that might be the inefficient protection by MAAs to act as sunscreen effect due to the small size of the cells (Bracher and Wiencke 1999).

Antarctic Polar Front

The Antarctic Polar Front was characterised by surface temperatures above 4°C and salinities lower than in the ACC outside of the frontal system (33.80-33.85). The water column was stratified with upper mixed layers between 15 and 35 m, and a phytoplankton bloom dominated by large or long chains of diatoms (at least 60-80% were diatoms and >20 μm) was found at the front (Bracher et al. 1999). Phytoplankton biomass was a bit lower than within the MIZ phytoplankton bloom (1-1.8 mg chl *a* m^{-3}). The chlorophyll maxima in the very centre were at 20-40 m, close to that at 40-60 m, and at the edge of the bloom rather evenly distributed from 0-50 m (Hense et al. 1998).

Within the euphotic zone about 60% in the blue spectral range of the attenuated light was absorbed by phytoplankton. This portion was highest where phytoplankton biomass was highest. Specific absorption of phytoplankton, a_ϕ*, was low because the amount of chlorophyll in a large cell is much higher than in a small cell. This results in an overall increase of absorption, but the value of the absorption normalised to chlorophyll, a_ϕ*, decreases (Bracher and Tilzer 1999). While within the APF chlorophyll values were always high, exceeding 1 mg chl *a* m^{-3}, primary production rates varied: Primary production rates and values of P^*_m were very high at the centre of the bloom, > 1000 mg C m^{-2} d^{-1} and >2.5 mg C *mg chl a^{-1} h^{-1}, respectively; those parameters decreased towards the edge of the bloom down to around 300 mg C m^{-2} d^{-1} and 1 mg C *mg chl *a* h^{-1} (Bracher et al. 1999, Strass et al. 1999). The same feature appeared at individual stations (Bracher et al. 1999) and in the mesoscale map in the area of the APF (Strass et al. 1999); since the on-line data (chlorophyll, underwater light climate- data) for this study were obtained at other days, there is some variation in the exact primary production values for one point, but overall values are in the same range (Bracher et al. 1999).

Maximum primary production rates were not significantly influenced by higher UVR corresponding to conditions inside the ozone hole. The amount of MAAs may be enough to work in combination with the large diameter of the big cells (*Thalassiothrix*) or the long chains (*Chaetoceros*, *Pseudonitzschia*) of phytoplankton as effective sunscreens; probably due to that and other UV protection mechanisms photoinhibition by enhanced UV radiation, seen in a lowering of quantum yield at PS II, could be compensated (Bracher and Wiencke 1999).

Table 3.1: Distribution of the various parameters into the different biogeochemical provinces: marginal ice zone (MIZ), Antarctic Circumpolar Current outside of frontal systems (ACC), Antarctic Polar Front (APF); some values are from the surface (0) and the 1% light depth (1%); all symbols are explained in the abbreviations (summary of results obtained in Bracher et al. 1999, Bracher and Tilzer 1999, Bracher and Wiencke 1999, Strass et al. 1999)

parameter	MIZ	ACC	APF
salinity	33.7	33.86-34.5	33.80-33.85
surface temperature [°C]	0.6	-1.5-<4	> 4
Z_{uml} [m]	<15	40-75	15-35
daylength [h]	20-24	14-20.5	16-17.5
daily maxima of E_o[PAR] [µmol q m^{-2} s^{-1}]	1000-2200	400-2200	900-1500
Z_{eu} [m]	40	45-90	28-50
K_d 490 [m^{-1}]	0.11	0.04-0.06	0.08-0.16
K_d 520 [m^{-1}]	0.11	0.06-0.07	0.09-0.12
K_d 665 [m^{-1}]	0.41	0.25-0.46	0.37-0.52
K_d 340 [m^{-1}]	0.41	0.12-0.14	0.19-0.35
K_d 380 [m^{-1}]	0.23	0.07-0.08	0.13-0.19
$\bar{a}_\phi$* (0) [m^2 mg chl *a* $^{-1}$]	0.014	0.016-0.027	0.006-0.017
$\bar{a}_\phi$* (1%) [m^2 mg chl *a* $^{-1}$]	0.007	0.018-0.030	0.006-0.018
a_ϕ*[440] at surface [m^2 * mg chl a^{-1}]	0.034	0.043-0.052	0.020-0.039
a_ϕ*[440] with depth [m^2 * mg chl a^{-1}]	<UML decreasing	constant	UML<20 m: decreasing
chl *a* in euphotic zone [mg chl *a* m^{-3}]	0.90-2.43	0.15-0.8	1.0-1.79
depth of chl *a* maximum [m]	0-15	40-80	20-60 *
dominating species	*Phaeocystis sp.*	none **	large diatoms
dominating size class among phytoplankton	>60%: >20µm	>70%: 2-20µm	>60%: >20µm
P^*_m (0) [mg C mg chl a^{-1} h^{-1}]	1.28	0.7-1.4	0.83-3.1
P^*_m (1%) [mg C mg chl a^{-1} h^{-1}]	1.06	0.27-3.2	1.30-3.2
α^*(0) [mg C mg chl a^{-1} h^{-1} (µmol q m^{-2} s^{-1})$^{-1}$]	0.0080	0.006-0.027	0.009-0.022
α^*(1%) [mg C mg chl a^{-1} h^{-1} (µmol q m^{-2} s^{-1})$^{-1}$]	0.014	0.015-0.05	0.014-0.032
E_k (0) [µmol q m^{-2} s^{-1}]	160	34-180	74-246
E_k (1%) [µmol q m^{-2} s^{-1}]	78	8-70	56-139
Φ_m (0) [mol C (mol photons)$^{-1}$]	0.014	0.010-0.024	0.024-0.035
Φ_m (1%) [mol C (mol photons)$^{-1}$]	0.047	0.020-0.058	0.040-0.093
ADP [mg C m^{-2} d^{-1}]	560	110-300***	300-1050*
effect of high UVR*** on P*m	no change	s.d.****	no change
effect of high UVR*** on F_v/F_m	s.d.****	s.d.****	s.d.****
MAAS conc. [µg MAAs l^{-1} (µg chl *a* l^{-1})$^{-1}$]	<0.5	3.8-8.0*****	2.5-3.9
number of sampled stations	1	10	13

* for details *see* text

** except in the South, close to ice edge: diatoms >40%

*** except in the South close, to ice edge: 390-480

**** s.d. = significant decrease

*****except in the South, close to ice edge: 1.2-1.7

4. GENERAL DISCUSSION

4.1 Introduction

This study provides first evidence that differences in biooptical characteristics coincide with the different biogeochemical provinces of the Southern Ocean, where the study was performed. The differences in biooptical characteristics were reflected in phytoplankton community structure, phytoplankton absorption characteristics, parameters describing the P versus E curve, and the underwater light field. Primary production rates were calculated taking into account all biooptical parameters studied in this thesis. Furthermore, factors influencing these parameters and primary production rates in the different biogeochemical provinces were determined, which also included studies on the effect of enhanced UV radiation due to ozone depletion on phytoplankton photosynthesis. Knowledge of global-scale features of phytoplankton biomass and productivity is crucial for the understanding of the Southern Ocean's role in the contemporary global carbon cycle (Sarmiento and Toggweiler 1984, Peng and Freyer 1987, Sarmiento et al. 1988, Fasham et al. 1990), and the relation between the distribution of primary producers and higher trophic-level consumers on a planetary scale. In the following sections, primary production and factors influencing it in the different biogeochemical provinces of the Southern Ocean (chapter 4.2), the specific biooptical parameters characterising these provinces (chapter 4.3), the methods used in this thesis (chapter 4.4), and the usage of our results to improve the calibration of ocean colour data received by remote sensing (chapter 4.5) and perspectives for the future (chapter 4.6) are discussed.

4.2 Biogeochemical provinces within the Southern Ocean

Within the Southern Ocean biogeochemical provinces can be defined which correspond broadly to different hydrographic regions. They are predominantly zonal. The hydrographic regimes are either characterised by fronts or interfrontal areas. The main current of the Southern Ocean is the Antarctic Circumpolar Current (ACC), which flows continuously around the Antarctic continent driven by the prevailing westerly winds. All the waters south of the Antarctic Polar Front (APF) constitute the Antarctic Ocean proper. The zone between the Subantarctic Front (SAF) in the north and the APF in the south is referred to as the Antarctic Polar Frontal Zone (APFZ). The APFZ, where flows like in the ACC are driven by west winds, is an area of downwelling, where the Antarctic Intermediate Water is formed. The winds over the Antarctic mainland are predominantly easterly winds, driving the coastal current. The transition of the eastwards flowing ACC and the westwards flowing coastal currents is referred to as the Antarctic Divergence (AD). Here, part of the deep North Atlantic water comes to the surface. The local anomaly in surface temperature, however, is low and not easily discernible. The marginal ice zone (MIZ) is defined as delimiting the influence of the input of low density melt water from the receding pack-ice and its southern border is marked by the shelf break. The coastal and continental shelf zone (CCSZ) constitues the ice free part of the continental shelf (Sievers and Nowlin 1988, Treguer and Jacques 1992, Orsi et al. 1995).

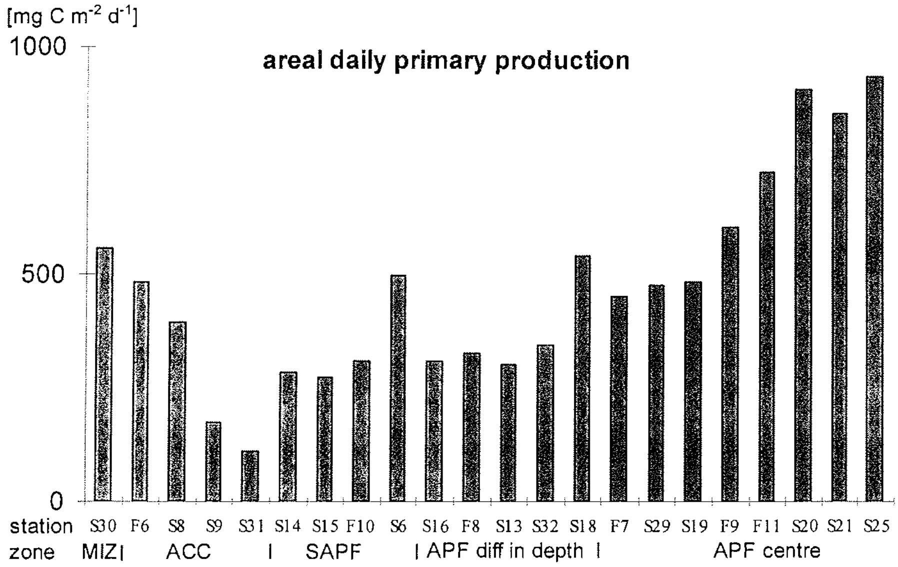

Fig. 4.1: Areal daily primary production rates at all stations in the Southern Ocean during ANT XIII/2; where SAPF = stations within the ACC, but just south of the APF, APF diff. (different) in depth = APF stations where P^*_m 1% light depth > P^*_m surface. APF centre = stations within the centre of the bloom. Figure was taken from Fig. 5 in Bracher et al. (1999)

Enhanced biomass and primary production have been found in the MIZ (Hart 1934, Smith and Nelson 1986, Sullivan et al. 1988, Comiso et al. 1990, Cota et al. 1992, Lancelot et al. 1993, Bracher et al. 1999- Fig. 4.1), in the shallow coastal waters and coastal polynyas (Comiso et al. 1990, Holm-Hansen and Mitchell 1991) and within the frontal areas (Kanda and Fukuchi 1979, Allanson et al. 1981, Tanimura 1981, Fukuchi and Tamura 1982, Lutjeharms 1985, Bidigare et al. 1986, Lutjeharms 1986, Laubscher et al. 1993, Bathmann et al. 1997, Bracher et al. 1999- Fig. 4.1) while the interfrontal areas show low values for both (Bracher et al. 1999- Fig. 4.1, and authors above); in this thesis we are focusing on the Antarctic Polar Front (APF), the ACC between Polar Front and MIZ (here referred as ACC) and the MIZ (Fig. 1.1).

4.2.1 Effects of the upper mixed layer on the formation of biogeochemical provinces

Sakshaug et al. (1991) have suggested a simple 1-dimensional-2-layer model to simulate the development of Antarctic spring blooms as a function of a) depth of the wind-mixed layer, b) light distribution in the water column, c) local meteorological conditions, d) size of initial standing stock, e) loss rate. Sakshaug´s model fits well with the dynamics of shade-adapted, large-celled bloom-forming diatoms. It demonstrates that during spring and summer, even with moderate loss rates, blooms are prevented from developing, as soon as the mixed-layer depth reaches 40-50 m (although blooms of prymnesiophytes have been reported in mixed layers of 80 m by Treguer and Jacques 1992).

The underwater light field, which phytoplankton encounter, is influenced by the upper mixed layer (UML) depth which is associated with the vertical stability of the water column. The mixed layer depth has great importance for the planktonic production process. Within a vertical light gradient phytoplankton adjust their photosynthetic characteristics to the local light level at different depths (Sakshaug and Slagstad 1991). In the Southern Ocean density stratification is caused by differences in salinity rather than in temperature. Strongly stratified regions have only been observed around land masses, in the MIZ and in an area of high stability at sloping frontal edges (Orsi et al. 1995). In accordance to the above described model by Sakshaug et al. (1991), waters with shallow and rather stable UML were found to be essential for the formation of Antarctic phytoplankton blooms (El-Sayed 1984, Smith and Nelson 1985, Legendre

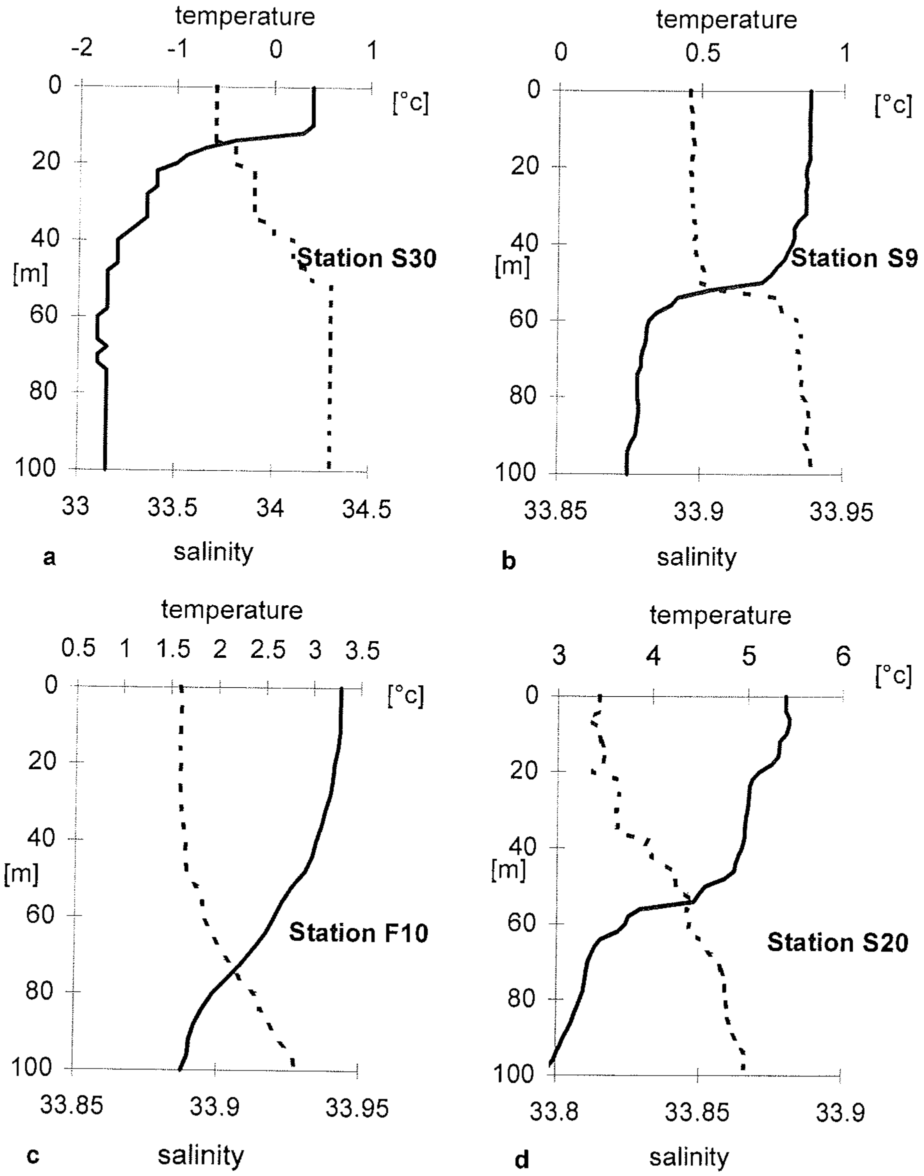

Fig. 4.2: Temperature (solid line) and salinity (dotted line) profiles in the Southern Ocean at several stations during ANTXIII/2: a) Station S30, MIZ; b) Station S9 as an example of the ACC; c) Station F10 as an example of the SAPF; d) Station S20 as an example of the APF. Data are obtained from CTD measurements by Strass et al. (1997) during ANTXIII/2. Figure was taken from Fig. 2 in Bracher et al. (1999)

1985, Perissinotto et al. 1990, Laubscher et al. 1993, Bracher et al. 1999- see Fig. 4.2). In shallow UMLs phytoplankton are held above the critical depth, which, compared to conditions at lower latitudes, have been suggested to be deeper in the Antarctic Ocean than under conditions of higher water temperatures; this has been inferred from the observation that respiration rates exhibited smaller temperature dependence than light-saturated photosynthesis (Tilzer and Dubinsky 1987). In contrast to that, weak vertical stability of surface water prevents phytoplankton from staying in the optimum light zone long enough for extensive production (Jacques 1989).

The differences in UML seem to be responsible directly or indirectly for most of the observed differences in phytoplankton physiology among the different provinces within the Southern Ocean (Bracher and Tilzer 1999, Bracher et al. 1999, Bracher and Wiencke 1999 and chapter 4.3). However, differences in UML depths within and outside the bloom at the Polar Front were not as clearly reflected when looking at the detailed map of primary production (Strass et al. 1999) as opposed to the survey only considering individual stations (Bracher et al. 1999, Tab. 3.1). This might be due to the temporal variance of obtaining data. Bathmann et al. (1997) observed during the first German JGOFS cruise phytoplankton blooms at the APF; substantial biomass often extended to depths below the shallow UMLs, where growth rates must have been light-limited. They suggested that despite the possibility of a fertilising effect by iron enhancement in this region, the blooms were facilitated earlier under favourable light conditions caused by shallow mixed layer depths. Hence, the phytoplankton distribution pattern was caused by the dynamics of the frontal zone which led to subduction of the surface layer.

The development of shallow UMLs within the two blooming areas, MIZ and APF, are caused differently. In the Marginal Ice Zone (MIZ) according to the seasonal cycle sea ice is forming and melting. The melting of the sea ice in spring and summer produces low salinity water. If this is not dispersed, the resultant buoyancy of the surface water produces a stable layer subject to high irradiance in which rapid growth may occur (Savidge et al. 1996). The Polar Front is the boundary of two main water masses; warmer waters from the mid-latitudes meet colder waters from the Antarctic area; the region is a site of substantial mesoscale activity, meanders and eddies are typical for this region (e.g. Gille and Kelly 1996). Taylor et al. (1978) has defined the Polar Front where the Antarctic surface water produces a circumpolar belt of minimum salinity at

200 m, which occurs generally one or two degree north of the surface discontinuity where the temperature minimum sinks. In the interfrontal areas deep UMLs or strong turbulences, seem to be responsible for no significant build-up of biomass (Savidge et al. 1996, Bracher et al. 1999). Although during the ANTXIII/2 expedition euphotic depths within the ACC were deeper than the UML depth (Bracher et al. 1999, Tab. 3.1), on cloudy days, which are very frequent in the Southern Ocean, phytoplankton were transported into layers too deep to obtain positive net primary productivity.

4.2.2 Effects by iron and silicate availability

Iron limitation has been proposed as a major factor responsible for the low production levels of Southern Ocean phytoplankton (Martin and Fitzwater 1988, Martin et al. 1989). Within the Southern Ocean iron concentrations are generally low (<1nM Fe) due to the marginal input by aeolian dust from the Antarctic continent since most of the land is covered by ice. Only in the areas with increased water column stability, iron availability is enhanced: While in coastal areas the shelf input from the continental crust forms an important source of iron for the seawater, a steady supply of iron via upwelling and lateral transport in frontal jets, forms an important source in remote areas of the Southern Ocean (de Baar et al. 1995). Iron is required by the photosynthetic apparatus for synthesis of several structural components (Glover 1977) and plays a role in reduction of nitrate to ammonium (Verstraete et al. 1980). Iron-enrichment experiments carried out by Van Leeuwe et al. (1997) on natural phytoplankton samples of the Southern Ocean indicate that they are not iron-starved *per se*, but iron stress leads to sub-optimal growth. During the first German JGOFS expedition to the Southern Ocean in 1992, iron concentrations appeared to govern distribution of phytoplankton biomass at the APF (de Baar et al. 1995), while during the second expedition in 1995/1996 iron concentrations remained low throughout the cruise and may have been responsible for maximum biomass and primary productivity below values obtained by optimum growth. However, the distribution of phytoplankton biomass and primary productivity was not determined by iron concentrations (de Jong et al. 1997).

It is widely accepted that phosphate and nitrate are not limiting factors for phytoplankton growth in the Southern Ocean (Holm-Hansen et al. 1977, Hayes et al. 1984, Jacques 1989, Laubscher et al. 1993). Nitrate, in particular, is always present in concentrations far in excess of phytoplankton demand, also during the ANTXIII/2 cruise (Hense et al. 1998). Of all nutrients, only north of the APF silicate concentrations were present which limit phytoplankton, especially diatom, growth (Allanson et al. 1981, Jacques 1989, Verlencar et al. 1990, Löscher et al. 1997, Hense et al. 1998). South of the Polar Front higher silicate concentrations could not stimulate growth there since the instability of the water column was too high.

4.2.3 Phytoplankton communities

Blooms which are typically observed in the vicinity of fronts and in the MIZ in the Southern Ocean, tend to be dominated by net-plankton (>20 μm), as opposed to the areas between fronts where mainly nanoplankton (<20 μm) form the community (Holm-Hansen and Mitchell 1991, Laubscher 1993, Bracher et al. 1999 - Fig. 4.3). Franks (1992) has claimed that due to the different swimming and buoyancy characteristics the phytoplankton are differentially advected at fronts, with the strongest swimmers away from the front. This hypothesis cannot explain the seasonal effect found by Laubscher et al. (1993): Only in early summer net-phytoplankton (>20 μm) was consistently the major components of the frontal blooms, while in late summer (March) phytoplankton community at the APF was mainly formed by nanoplankton and major net-phytoplankton blooms were only encountered south of the APF where silicate levels exceed 20 μM.

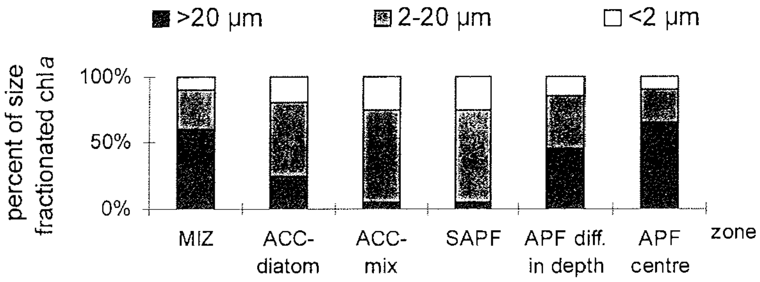

Fig. 4.3: Size fractionated (>20 μm, 2-20 μm and <2 μm) chl *a* concentrations within the euphotic zone from ANTXIII/2 where SAPF = stations within the ACC, but just south of the APF, APF diff. (different) in depth = APF stations where P^*_m 1% light depth > P^*_m surface; ACC diatom = ACC stations close to the ice edge with a high portion of diatoms in the phytoplankton community, and ACC mix = ACC stations with equal contributions of phytoplankton groups in the community. Figure was taken from Fig. 3 in Bracher et al. (1999)

The netplankton which form Antarctic phytoplankton blooms mainly consists of large-celled and colonial diatoms (e.g. El-Sayed and Taguchi 1981, Jacques 1983, von Bröckel 1985, El-Sayed and Weber 1985, Heywood and Priddle 1987, Bianchi et al. 1992, Crawford 1995, Savidge et al. 1995, bloom at the APF in Bracher et al. 1999 - Fig. 4.3 and Fig. 4.4 or Hense et al. 1998). Blooms formed by *Phaeocystis* colonies are often observed in the coastal and continental shelf zone (CCSZ), especially at the western Ross Sea (e.g. Palmisano et al. 1986) and the Weddell Sea (Hayes et al. 1984, Nöthig 1988), but also often form the second period of MIZ blooms (Karsten 1905, Hart 1942, El-Sayed 1984, Garrison et al. 1987, Fryxell 1989, Smetacek et al. 1990, Jacques and Panouse 1991, Stöcker 1995, Bracher et al. 1999 - Fig. 4.3 and Fig. 4.4). The second period of blooms at fronts north of the APF are formed by nanoplankton (Laubscher et al. 1993).

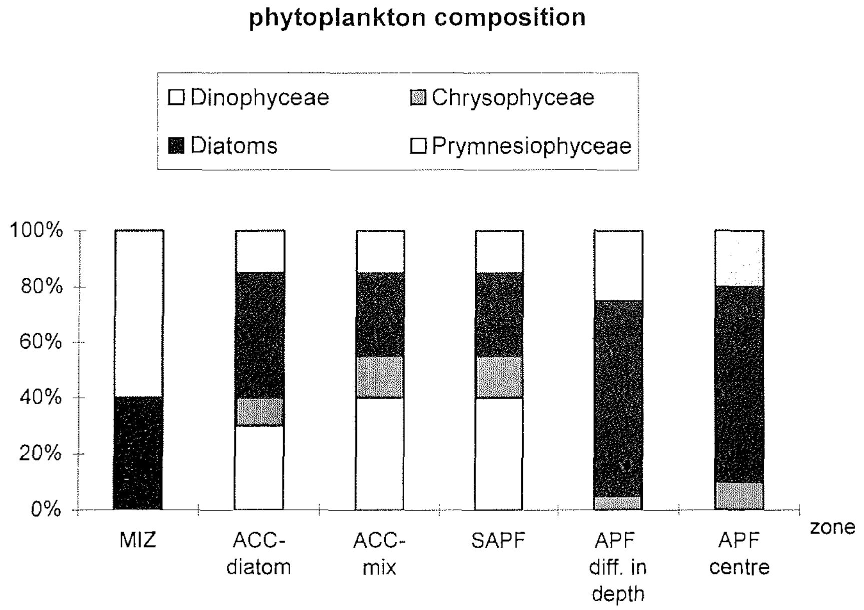

Fig. 4.4: Phytoplankton composition within the different areas from ANTXIII/2. Ratios (%) of each algal group were obtained according to the method described in Bracher et al. (1999) by converting characteristic accessory pigment concentrations to chl *a* and relating it to the total extracted chl-a. All pigments for this calculation were determined by HPLC analyses. SAPF = stations within the ACC, but just south of the APF, APF diff. (different) in depth = stations in this area where the P^*_m values from 1% light depth were significantly higher than at the surface. ACC diatom = stations in the area of the ACC close to the ice edge with a high portion of diatoms in the phytoplankton community. ACC mix = stations in the area of the ACC with equal contributions of phytoplankton groups in the community. Figure was taken from Fig. 3 in Bracher et al. (1999)

At the second German JGOFS cruise the variation of phytoplankton biomass distribution in the various size classes corresponded to the distribution of grazers in different size classes (Dubischar and Bathmann 1998): within the APF growth of small phyotplankton (< 20 µm) seemed to be suppressed by grazing of large numbers of small cyclopoids, while in the ACC the bigger calanoids were five times more abundant and putting high grazing pressure on larger phytoplankton. Still, the long spines (especially *Chaetoceros* spp.) and big frustules (esp. *Thalassiothrix* sp.) of the dominating species at the APF bloom may act as efficient protectors against grazing pressure, and therefore the disadvantage of growing slower can be compensated in shallower UMLs (Schültke 1998).

4.2.4 Contribution of different regions on total biomass of the Southern Ocean

The positive correlation of phytoplankton productivity and biomass observed by the same three-dimensional map of the APF (Strass et al. 1999 - Fig. 4.5), points out the importance of the initial chlorophyll distribution when environmental conditions become favourable for growth. Most studies indicate increased biomass and productivity at the APF (*see* chapter 4.2), but there have been reports of poor productivity (El-Sayed 1984, Verlencar et al. 1990, Laubscher et al. 1993). A seasonal trend of chlorophyll concentrations at the APF has been observed by several studies (Fukuchi and Tamura 1982, Wantanabe and Nakajima 1983, Sasaki 1984, Laubscher et al. 1993), which were high in early summer, but low in late summer with a shift in the area of maximum biomass to the south of the APF. Ice-edge blooms have been found due to evaluating remotely sensed ocean colour data, not only to be a spring-summer feature, but also extent into austral autumn (Comiso et al. 1990). However, recent studies in the JGOFS programme have reinvestigated ice-edge systems and found that blooms of the type described may not always appear; Turner and Owens (1995) and Bathmann et al. (1997) have demonstrated the absence of stability-induced phytoplankton blooms associated with the MIZ in the open waters of the Southern Ocean at 6°W and in the Bellinghausen Sea, respectively. Still even when only regarding 25 % of the MIZ forming blooms, Savidge et al. (1996) calculated in their model that the contribution of the MIZ to the Southern Ocean's biomass is still significant: looking at the area within the Southern Ocean from the Subantarctic Front (SAF) to the south, the specific contributions of the three zones to the overall biomass are the following: APF 5-10%, MIZ 20% and ACC (from APF to MIZ) 30%. These numbers diminish to 50% of their value when considering the area within the Southern Ocean south from the Sub-Tropical Convergence.

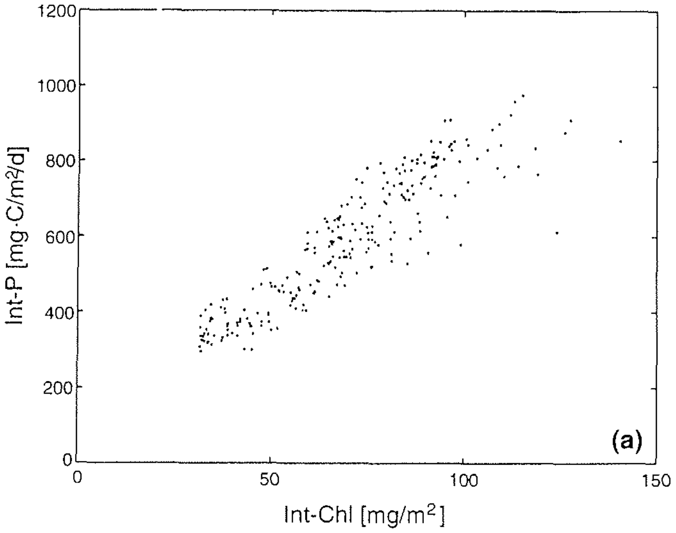

Fig. 4.5: Scatter diagram of vertically integrated production (Int-P) versus chlorophyll content (vertically integrated chlorophyll concentration (Int-Chl) within the APF and the SAPF during the ANT XIII-2 cruise. Figure was taken from Fig. 9a in Strass et al. (1999)

4.3 Biooptical characteristics of phytoplankton

Regional differences in biooptical characteristics have been observed among phytoplankton, regarding overall absorption, specific absorption coefficient (both Bracher and Tilzer 1999), quantum yield of carbon fixation (Bracher et al. 1999), sunscreen effect of UV absorbing compounds, and sensitivity to enhanced UVR (Bracher and Wiencke 1999) which are mainly due to species composition, size of phytoplankton cells, chains or colonies, and overall biomass (Bracher et al. 1999). Factors influencing these phytoplankton characteristics are mainly the depth of the upper mixed layer and the rate of vertical mixing (Bracher and Tilzer 1999, Bracher et al. 1999, Bracher and Wiencke 1999) and differences in grazing pressure (Dubischar and Bathmann 1998, *see* Bracher et al. 1999).

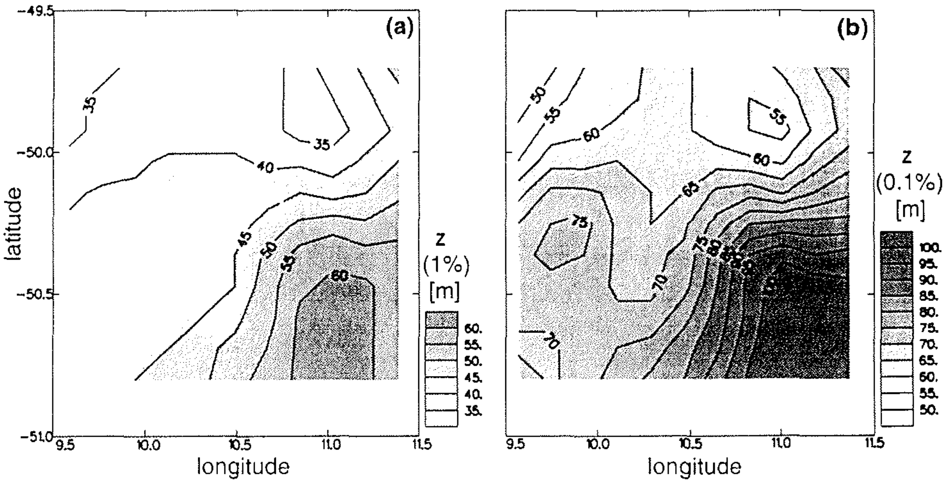

Fig. 4.6: Horizontal distribution of (a) the 1 % and (b) the 0.1 % light depth of PAR within the APF and the SAPF during the ANT XIII-2 cruise. Figure was taken from Fig. 2 in Strass et al. (1999)

4.3.1 Light attenuation by phytoplankton

When biomass reaches a certain value, self shading is lowering the rate of capturing photons for photosynthesis.This results in a mesoscale variation of the different light depths roughly by a factor of 2-3 (Bracher and Tilzer 1999 - Fig. 2.1 and Strass et al. 1999 - Fig. 4.6). However, blooms within the Southern Ocean as compared to ones in lower latitudes are moderate and self shading is smaller. In addition, non-algal substances in Antarctic waters are mainly derived from autochthonous sources since there is hardly any input of terrestrial material from the Antarctic continent. Concentrations and attenuation of these materials are found to be particularly low (Mitchell 1992, Tilzer et al. 1994, Bracher and Tilzer 1999 - Fig. 4.7). Therefore, the fractional light attenuation by phytoplankton within the blue spectrum is higher in Southern Ocean blooms (>60% in Bracher and Tilzer 1999 - Fig. 4.8, Tilzer et al. 1994), compared to blooms at lower latitudes and the Arctic (Mitchell 1992, Kirk 1994a). Outside of blooms the portion still remains 25%. Within the vertical component, the effect of water absorbing nearly everything in the red spectrum already below surface, is ensued by increasing absorbance of phytoplankton with depth. This feature gets eroded when the phytoplankton biomass reaches a certain value (above 1 mg chl *a* m^{-3}); under these circumstances biomass determines the depth of maximal absorption by phytoplankton (Bracher and Tilzer 1999 - Fig. 4.9).

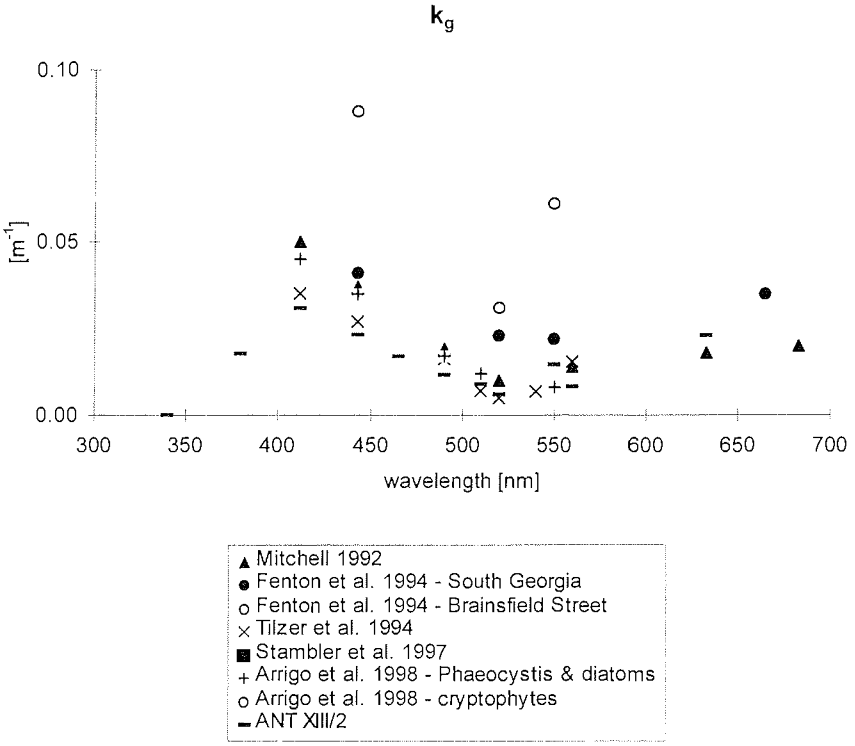

Fig. 4.7: Comparison of k_g values from the during the ANT XIII-2 cruise and literature. Figure was taken from Fig. 12a in Bracher and Tilzer (1999)

4.3.2 Specific absorption by phytoplankton

The chlorophyll specific absorption by phytoplankton, $a_{\phi}^{*}[\lambda]$, at any given wavelength is a variable depending on pigment composition and pigment packaging. In our study $a_{\phi}^{*}[\lambda]$ varied widely, at least two-fold at 440 nm which is the wavelength of maximum absorption by the majority of pigments. The pigment composition in natural samples is influenced by the species composition itself, but also responds to the light environment algal cells encounter. The package effect depends on cell size, shape, cellular pigment composition, the number and shapes of chloroplasts, and thylakoid stacking. This is manifested as a decrease in $a_{\phi}^{*}[\lambda]$ with increasing chl *a* concentration per cell and with increasing chl *a* C^{-1} ratios (Dubinsky et al. 1986). In cells acclimated to low-light, $a_\phi{}^*[\lambda]$ is generally lowest which is described to the package effect (Morel and Bricaud 1986, Dubinsky 1992, Johnsen and Sakshaug 1993, Kirk 1994a, Bracher and Tilzer 1999). These cells, compared to cells acclimated to high-light, are packed with more photosynthetic pigments. By that the number of photons captured increases which is

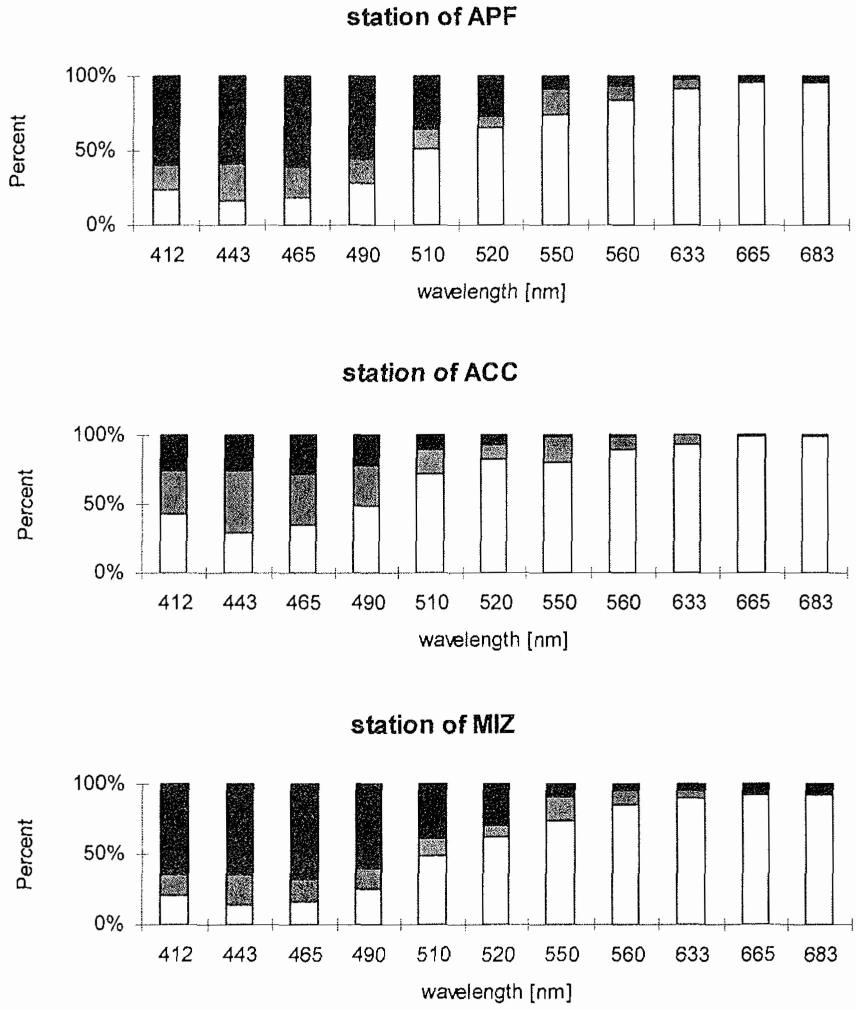

Fig. 4.8: Contributions of pure water (white), non-algal material (grey) and phytoplankton (black) to light attenuation as a function of wavelength at low (b) a station within the ACC with 29 mg chl *a* m^{-2}) and at high (a station a) within the APF with 122 and c) within the MIZ with 95 mg chl *a* m^{-2}) phytoplankton biomass during the ANT XIII-2 cruise. Figure was taken from Fig. 8 in Bracher and Tilzer (1999)

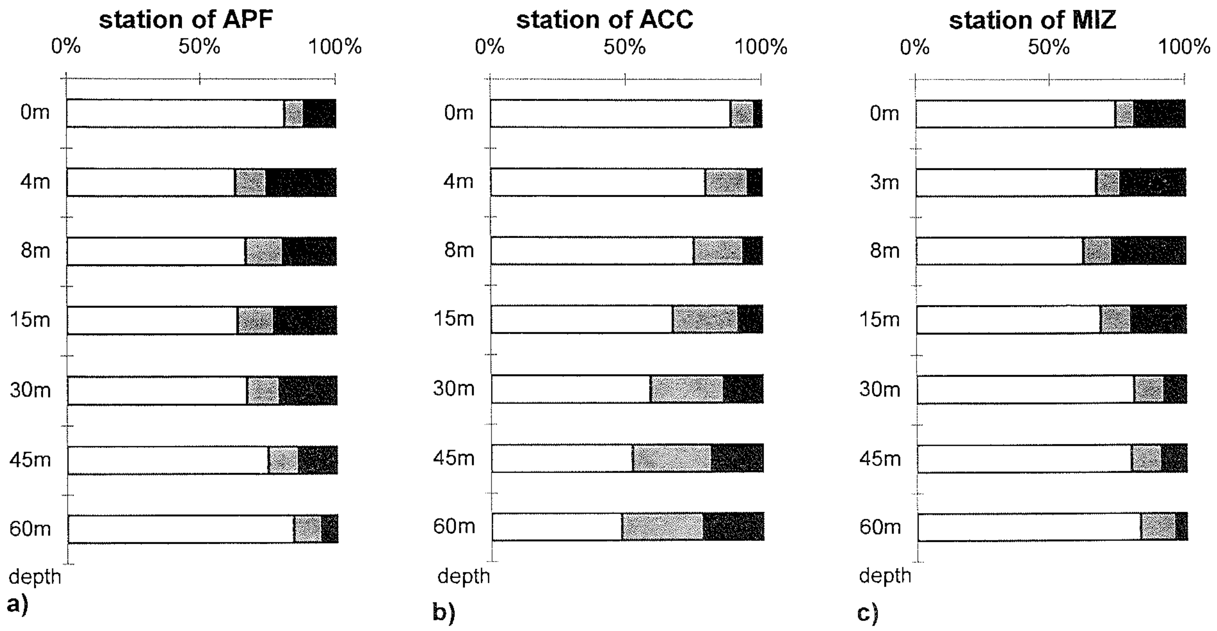

Fig. 4.9: Vertical profiles of the relative contributions of pure water (white), non-algal material (grey) and phytoplankton (black) to light attenuation of underwater PAR. The portion of phytoplankton in total light attenuation is a measure of light harvesting by phytoplankton. a) a station within the APF, b) a station within the ACC and c) a station within the MIZ during the ANT XIII-2 cruise. Figure was taken from Fig. 9 in Bracher and Tilzer (1999)

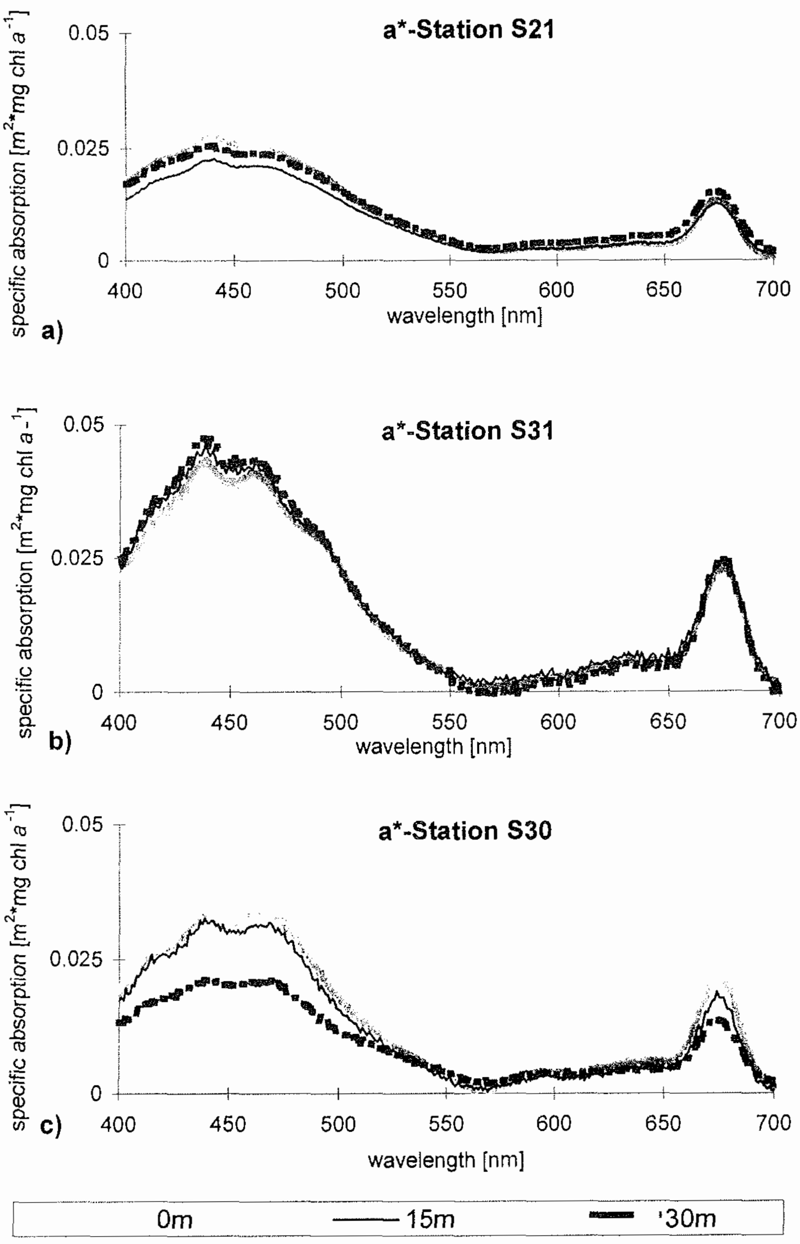

Fig. 4.10: Spectra of specific absorption a_ϕ* (absorption of phytoplankton normalised to chl *a*) at three representative stations: a) Station S21 for the APF, b) Station S31 for the ACC and c) Station S30 for the MIZ during the ANT XIII-2 cruise. Figure was taken from Fig. 10 in Bracher and Tilzer (1999)

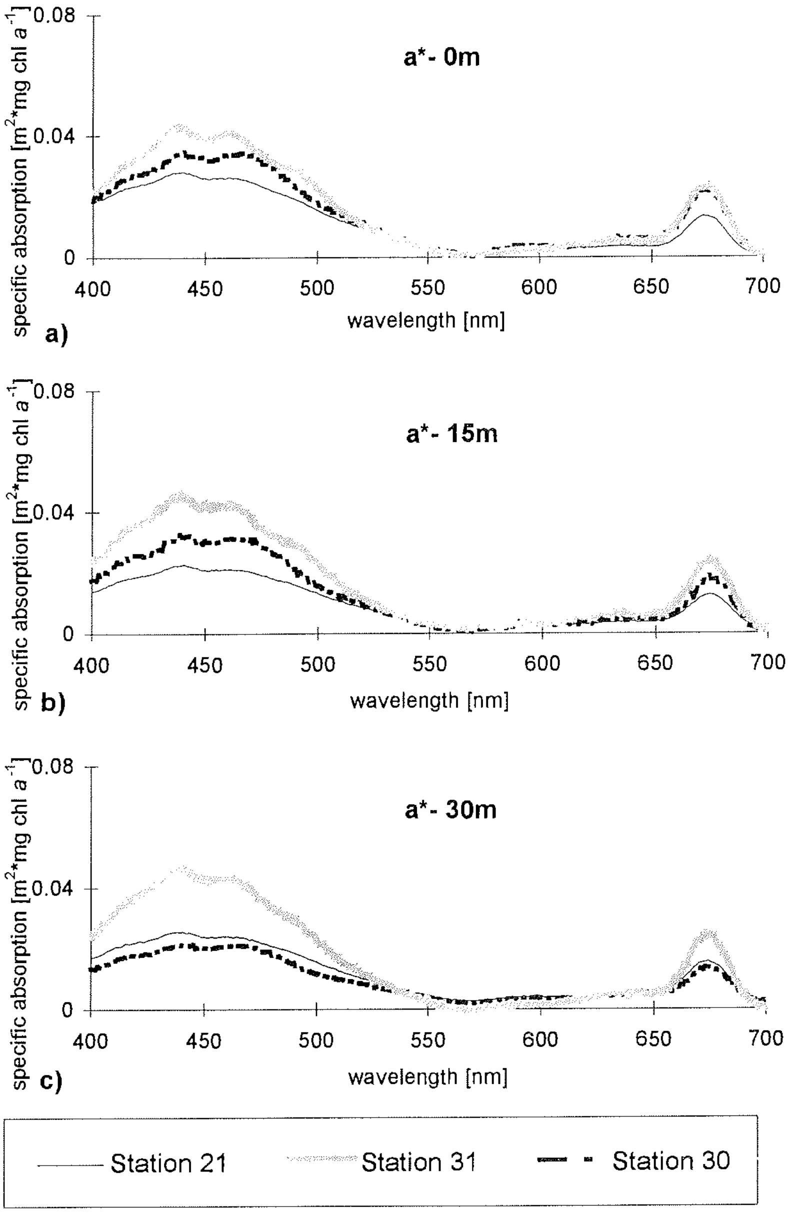

Fig. 4.11: Spectra of specific absorption a_ϕ* (absorption of phytoplankton normalised to chl *a*) at three representative stations: Station S21 for the APF, Station S31 for the ACC and Station S30 for the MIZ at a) 0m, b) 15m and c) 30m during the ANT XIII-2 cruise. Figure was taken from Fig. 11 in Bracher and Tilzer (1999)

important under low light conditions; but, on the whole the efficiency of capturing photons decreases. In addition to that, pigment packaging varies with cell size; large cells are stacking more pigments per cell than small cells (Johnsen and Sakshaug 1993, Johnsen et al. 1994).

Acclimation to low light was observed at the station within the MIZ bloom and three stations within the APF bloom where the upper mixed layer was very shallow (<20 m). The $a_\phi*[\lambda]$ values in phytoplankton samples from below the UML were significantly lower compared to samples from depths above, while the pigment composition within the water column did not significantly change (Bracher and Tilzer 1999 - Fig. 4.10). At those sites, still 15-30% of the daily primary production rate was fixed below the UML depth (Bracher et al. 1999).

We also observed a difference in $a_\phi*[\lambda]$ between phytoplankton of the different areas due to cell size and species specific pigment composition (Bracher and Tilzer 1999 - Fig. 4.11 and Bracher et al. 1999 - Fig. 4.3 and Fig. 4.4). Lower values of $a_\phi*[\lambda]$ were seen in the bloom samples where either the cells themselves were bigger or they were combined in long chains (diatoms) or colonies (*Phaeocystis*). Small cells having less pigments per cell are more efficient in capturing light than big cells. Due to the principle that bigger bodies have a smaller surface area than smaller ones, more pigments per cell are necessary in such bodies to encounter the same amount of photons as small bodies (Johnsen et al. 1994).

4.3.3 Quantum yield

The maximal quantum yield of photosynthesis, Φ_m, indicates the conversion of absorbed light energy to chemical energy and is a measure which depends besides on $\alpha*$, also on $\bar{a}_\phi*$, the spectrally weighted absorption coefficient of phytoplankton for PAR, which is influenced by $a_\phi*[\lambda]$ (*see* chapter 2.4). According to Morel (1978) the Φ_m value for green eutrophic waters are on average higher than those observed in blue, oligotrophic waters. Cleveland et al. (1989) observed under bloom conditions for short photosynthetic incubations, which minimise respiration of newly fixed carbon, Φ_m for nitrogen-replete cells to approach maximal theoretical values (0.062-0.102 for 3-20 m) In contrast, when they revisited the location two weeks later, the nitracline was deeper and the phytoplankton appeared to be in post-bloom conditions which was indicated by higher phaeopigment concentrations and much lower Φ_m values (0.033-0.044 at 3-20 m). In general, our results showed higher values in the blooming areas as opposed to the non bloom areas, except for the values within the MIZ bloom (Bracher et al. 1999 - Fig. 3.1). Here Φ_m values , especially for the surface samples were even lower than in the ACC outside the APF. According to Cleveland et al. (1989) these low Φ_m values in addition to the POC:PON and chl *a*: phaeo *a* ratios indicate that the final phase of the bloom has started (*see* Bracher et al. 1999).

4.3.4 Sensitivity to enhanced UVR

An impact of increased levels of UVR to primary production of natural phytoplankton within the Southern Ocean has been measured by several studies (El-Sayed et al. 1990, Smith et al. 1992, Lesser et al. 1996, Neale et al. 1998, Bracher and Wiencke 1999). The balance between UV-B damage and repair of damaged sites is a non-linear function that is sensitive to the physiological state of the phytoplankton (Cullen and Lesser 1991, Lesser et al. 1994, Bracher and Wiencke 1999). Furthermore, laboratory and field studies indicate that algal sensitivity to UV-B appears to be species-specific (Jokiel and York 1984, Karentz et al. 1991a, Smith et al. 1992, Davidson and Marchant 1994), in dependence of phytoplankton cell size (Garcia-Pichel 1994, Bracher and Wiencke 1999) and underwater light field (Helbling et al. 1994, Bracher and Wiencke 1999).

The depth of the upper mixed layer and the rate of mixing determine the underwater light field. The ratio of UV-A/UV-B and blue light/UV-B increases with depth (Smith et al. 1992). Cullen and Lesser (1991) have shown that for an equal dose of UV-B, short exposure to high irradiance is more damaging than longer exposure to lower irradiance. Therefore, UVR damage can be acute to phytoplankton approaching the surface in a water column with a high mixing rate.

The information given by F_v/F_m value is an estimate of the maximum quantum yield of electron transport in photosystem II (i. e. excitation capture by open PSII centres) and can be used to assess the photosynthetic conversion efficiencies of phytoplankton (Schreiber et al. 1995). Simultaneous measurement of the ratio of variable to maximum fluorescence (F_v/F_m) of dark acclimated algae and carbon fixation rates helped to

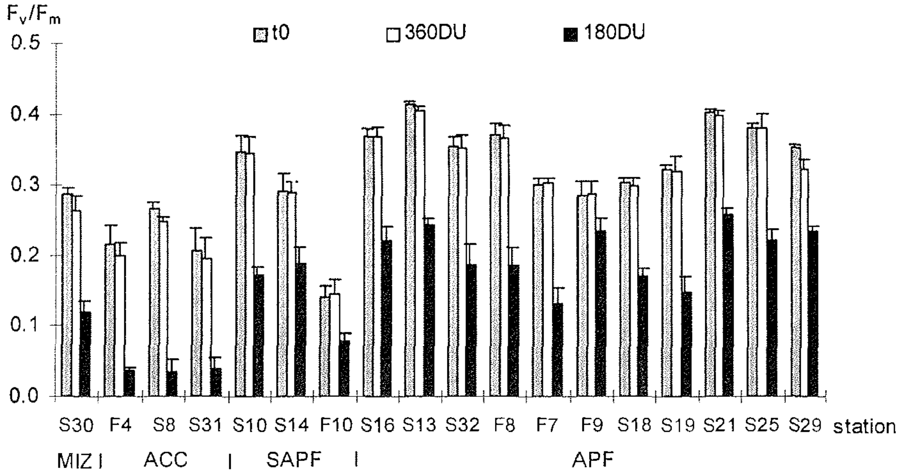

Fig. 4.12: Quantum yield of electron transport in PSII, F_v/F_m, at surface water samples after sampling (t0), after four hours of incubation under a spectrum corresponding to an irradiance field encountered in 5 m depth under depleted (180 DU) and normal ozone concentrations (360 DU) during the ANT XIII-2 cruise. Stations are grouped to the areas within the Atlantic sector of the Southern Ocean which they are located in: MIZ, ACC, SAPF, APF. Figure was taken from Fig. 5 in Bracher and Wiencke (1999)

elucidate the different inhibitory processes affecting photosynthetic rates (Bracher and Wiencke 1999 - Fig. 4.12 and Fig. 4.13). While dynamic photoinhibition is a process of photoprotection, the chronic photoinhibition implies damage within the cell (Osmond 1994). All phytoplankton samples were sensitive to irradiance conditions inside the ozone hole, seen in a lowering of F_v/F_m. In samples taken from sites within the phytoplankton bloom primary production rates remained at values similar to those measured under conditions outside the ozone hole which indicates dynamic photoinhibition according to new definitions by Osmond (1994); photosynthesis was actively downregulated for a short time and the cells were efficiently protected from further negative effects of UV-B. Dynamic photoinhibition amplifies the non-photochemical energy dissipation by converting the excessive absorbed energy into thermal radiation and is probably controlled under participation of certain carotenoids by the xanthophyll cycle (Krause and Weis 1991, Hanelt 1996). Strong lowering of carbon fixation rates in phytoplankton from outside the bloom areas indicate passively induced damage or at least chronic inhibition by enhanced UVR. Besides the degradation of the D_1 protein, probably ribulose biphosphate carboxylase / oxygenase

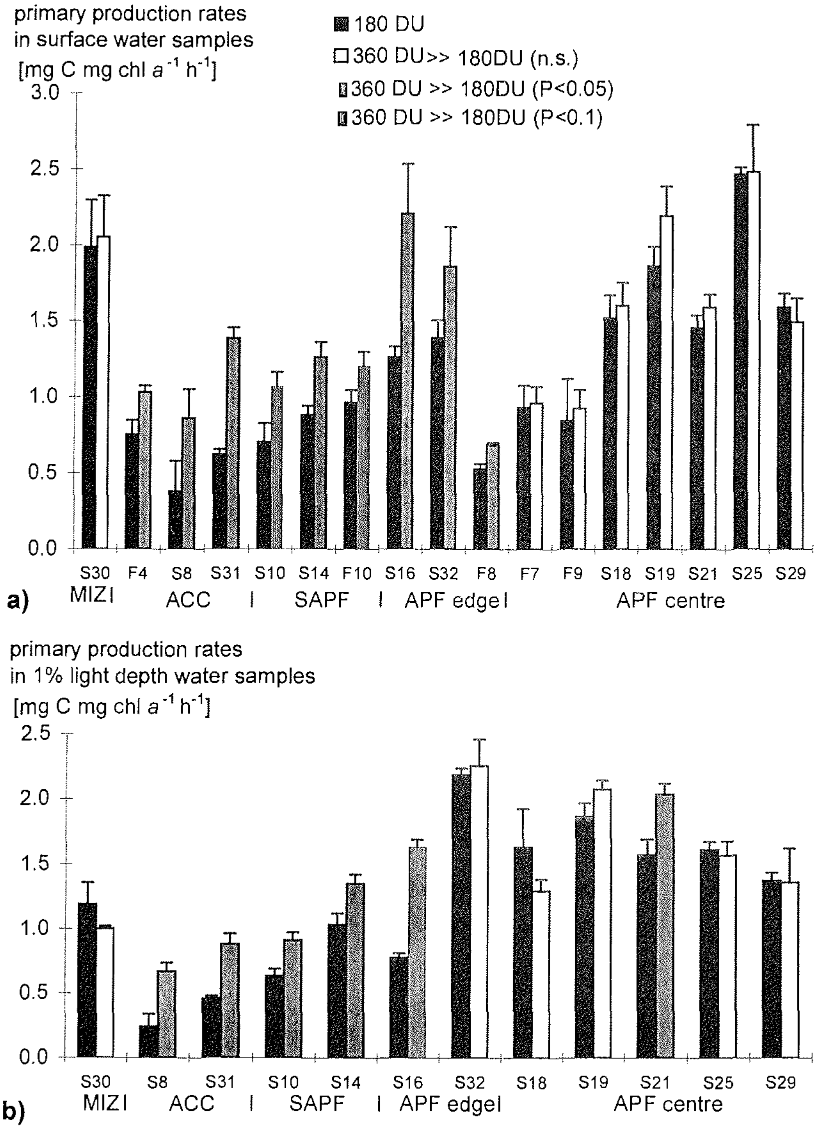

Fig. 4.13: Primary production rates after four hour incubation under a spectrum corresponding to an irradiance field encountered in 5 m depth under depleted (180 DU) and normal ozone concentrations (360 DU) a) in surface water samples and b) in 1% light depth water samples during the ANT XIII-2 cruise. Stations showing a significant higher production rate under conditions under normal ozone concentrations as compared to depleted ozone concentrations (360 DU >> 180DU) are indicated with grey colour ($P<0.05$), with grey stripes when P was only <0.1, with white colour when there was no significant difference between the two. Stations are grouped to the areas within the Atlantic sector of the Southern Ocean they which are located in: MIZ, ACC, SAPF, APF edge (within the APF, with high biomass but already low surface temperatures), APF centre. Figure was taken from Fig. 6 in Bracher and Wiencke (1999)

(RUBISCO) was down regulated (as shown *in* Lesser et al. 1996). Fast recovery as seen in the bloom sites indicates photoprotection mechanisms, whereas photodamaged proteins and pigments require several days for repair (Hanelt et al. 1992).

Besides quenching by dynamic photoinhibition, other strategies are known to reduce deleterious impacts of UVR to phytoplankton (for overview *see* Vincent and Roy 1993). An increasing number of naturally occurring compounds have been identified that absorb strongly in the UV-A and UV-B region of the spectrum. Their increase in cellular concentration under conditions of elevated UV dosages has taken to imply that they are produced as natural sunscreens, but it remains possible, that they play additional, as yet unknown roles. In phytoplankton, as UV-absorbing compounds, different mycosporine like amino acids (MAAs) have been identified, which absorb maximally in the range 310 to 360 nm (Carreto et al. 1990, Karentz et al. 1991b). In many cyanobacterial organisms scytonemin has been identified as a pigment which absorbs mainly in the UV-A region (e.g. Turian 1985). Carotenoids are also involved in another quenching mechanism besides the dynamic photoinhibition process. By the interaction of UVR and oxygen, toxic intermediates are produced which can be more damaging than the UV exposure itself. In addition to various enzymatic defences (Shibata et al. 1991), carotenoids can detoxify these radical intermediates by acting as general radical-trapping antioxidants (Burton and Ingold 1984). Repair mechanisms have been well studied for DNA damage and the photosystem II reaction centre. The repair system of PSII (Greenberg et al. 1989) and the induction of UV absorbing compounds (e.g. MAAs) synthesis (Riegger and Robinson 1997) are light controlled processes which work under PAR- or UV-A + PAR (especially blue light) irradiance. When mixing rates and depths are optimally, cells are held long enough in depths without UV-B, but where still enough UV-A and blue light is encountered; thus induction of MAAs and turnover rates of recovery in phytoplankton photosynthesis can compensate the UV damage.

It is important to note, that the sunscreen effect of MAAs is not only dependent on the amount of compounds synthesised, but also on the size of the cells (Garcia-Pichel 1994). Only within the blooms the phytoplankton cells were large enough (Fig. 4.3) that MAAs were acting efficiently in protecting against deleterious UVR (according to the definition of Garcia-Pichel 1994). Although outside the blooms phytoplankton contained the greatest amount of MAAs in our study (Bracher and Wiencke 1999 - Fig. 4.14), MAAs could not protect efficiently the cells because of the small size of the cells (90% <20 µm; Fig. 4.3). According to Garcia-Pichel at this size class only an investment >10% of the dry biomass can give efficient protection to UVR. Additional UV protection within the bloom areas may have been obtained by self shading and higher turnover rates of the various repair mechanisms due to the rate and depth of mixing. Species differences in sensitivity of induction processes have been found among diatoms and *Phaeocystis antarctica* for MAA synthesis (Riegger and Robinson 1997), they may also be different for other protection mechanisms and other phytoplankton species (and groups).

In summary, primary production in our study area from the APF south to the MIZ, seemed to be stronger impaired by enhanced levels of UVR outside of phytoplankton blooms than within.

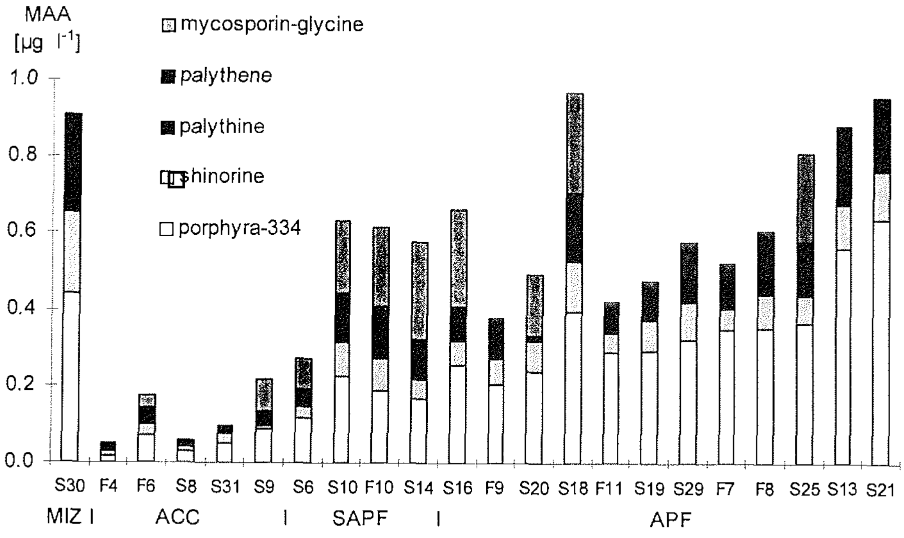

Fig. 4.14: MAAs (mycosporine-glycine, porphyra-334, shinorine, palythine, palythene) measured by HPLC analysis during the ANT XIII-2 cruise. Stations are grouped to the areas within the Atlantic sector of the Southern Ocean which they are located in: MIZ, ACC, SAPF, APF. Figure was taken from Fig. 7a in Bracher and Wiencke (1999)

4.4 Methodological aspects

In this thesis a simultaneous insight in biooptical processes determining primary production was given. Primary production data were obtained from the same natural samples by a detailed resolution of spectral compartments (4.4.1) using different scales and techniques (4.4.2).

4.4.1 Spectral resolution of underwater light field and absorbance characteristics

The resolution of the underwater light field and the phytoplankton absorption characteristics on a spectral scale is necessary when primary production rates are derived from P versus E incubations under an artificial light source. Both characteristics are of great importance for modeling primary production on the basis of pigment concentrations revealed by remote sensing. This is because relationships between the underwater light climate and algal photosynthesis are not determined by light intensity only, but also by light quality.

Data on the spectral resolution of the underwater light field were used to compare the different compartments in the water attributing to the attenuation of light. The increase of $\bar{a}_{\phi}*$ with depth regardless of chlorophyll concentration due to the strong attenuation of water in the red spectral range at the sea surface has to be taken into account when estimating pigment concentration from reflectance data.

The comparison of two measures characterising the influence of phytoplankton on the attenuation of light (for definitions *see* chapter 2.1 and 2.3) lead us to conclude that measuring the chlorophyll specific absorption coefficient, $a_{\phi}*[\lambda]$, is important when using remote sensing ocean colour data for determining pigment concentration and primary production. While only one value of the specific attenuation coefficient, $k_c[\lambda]$, could be determined for all stations, $a_{\phi}*[\lambda]$ was determined for each station at six depths. The determination of $k_c[\lambda]$ has the following disadvantages (*see* Bracher and Tilzer 1999): at wavelengths > 600 nm due to Ramnan scattering (Stavn and Weidmann 1990) no $k_c[\lambda]$ values can be obtained. Regional differences in $k_c[\lambda]$ can only be obtained with an extensive sampling; no separate values are determined over depth, thus photoacclimation can not be studied. The contribution of phytoplankton is overestimated by $k_c[\lambda]$ due to non-algal substances which are still influenced by the amount of chlorophyll (Häse 1996); the correction of a[λ] by $a_d[\lambda]$ to derive a_ϕ [λ] (and by that a_ϕ *[λ]) seems to be much more accurate.

In addition, the spectral resolution of the underwater light field, $E_d[\lambda]$, and $a_\phi*[\lambda]$ are "ingredients" for determining the spectrally weighted absorption coefficient of phytoplankton for PAR, $\bar{a}_\phi*$. Usually this value is necessary for correcting α, when α was obtained in a P versus E curve not performed under a natural light climate. Errors due to not correcting α are pointed out in Bracher et al. 1999 (Table 4). Also the parameter Φ_m is calculated with α and $\bar{a}_\phi*$.

Table 4.1: Comparison of ADP rates during ANT XIII-2 cruise calculated in our study including spectral correction of $\alpha*$ to not spectrally weighting $\alpha*$ (= not corrected). Table was taken from Table 4 from Bracher et al. 1999

	$\alpha*$ not corrected
n	22
min-max	59%-108%
mean	80%
stdev	9%

Different intercalibrations between instruments were necessary for the calculation of areal daily primary production (ADP) rates in Bracher et al. (1999) and Strass et al. (1999). Most important was the conversion of underwater PAR measured in W m^{-2} with the SeaSoar light meter to μmol quanta m^{-2} s^{-1}, since each photon captured by plants influences the photosynthetic pathway in the same way regardless of its energy content. For this conversion the spectral resolution of the underwater light field measured by the MER underwater light meter on all stations within the grid of the map were used. The information on photons captured for photosynthesis is indispensable for comparison to other studies.

Due to the knowledge of the spectral composition of the underwater light field in dependence to the stratospheric ozone layer an incubator was constructed simulating natural irradiance conditions within the water column (Tüg 1996, Abele-Oeschger et al. 1997). In this incubator the same sample was incubated under irradiance conditions inside and outside the ozone hole and the "real" effect of enhanced UVR due to ozone depletion was studied. In previous studies either parts of the natural irradiance fields have been cut off (El-Sayed et al. 1990, Neale et al. 1992, Smith et al. 1992, Helbling et al. 1992, Boucher and Prezelin 1996, Helbling et al. 1996), or, as often under artificial light sources, the UV radiation has been far too strong as compared to the natural conditions (Cullen and Lesser 1991, Davidson and Marchant 1994, 1996), or, different samples were incubated under the natural sun spectrum in- and outside the ozone hole (Smith et al. 1992). Since photoinhibition of photosynthesis by a specific wavelength (290 to 700 nm in nature) at any given time is a function of polychromatic damage and repair processes within an algal cell (Cullen et al. 1992), a small difference between an incubation spectrum and a natural sunlight spectrum may produce arbitrary results.

4.4.2 Areal daily primary production rates

There are different ways to estimate primary production in the sea: direct measurements on natural phytoplankton samples are the "basis" for all further calculations and models. Resolving primary production on a mesoscale or small scale can be done in addition of either using on-line underwater fluorescence and light data obtained by a towed undulating instrument (e.g. SeaSoar) or using reflectance data from remote sensing (*see* 4.5).

Different methods exist for direct measurements of primary production. In algal cultures, carbon uptake must be lower than rates for oxygen evolution (*see* chapter 2.4). However, for natural samples, the oxygen budget of a P versus E sample, or a body of water, is related to the net community production, i.e. the gross photosynthesis minus respiratory losses in all organisms, heterotrophs included (Sakshaug et al. 1997). This makes it difficult to detect the small changes that arise, due to photosynthesis, in oxygen concentration after short (<24 h) incubations, except under bloom conditions (Williams et al. 1996). In addition, the ^{14}C method has a high sensitivity in oligotrophic waters, where the oxygen measurements soon reach their detection limit. Fluorescence measurements provide only information on mechanisms underlying variations in carbon assimilation and no discrete numbers of carbon fixation rates can be derived. Therefore, we focus in this chapter on measurements of carbon uptake.

Three incubation methods are common: a) the *in situ*, b) the simulated *in situ*, and c) the *in vitro* incubation. On expedition ANT XIII/2 the simulated *in situ* (Tremblay 1997) and the *in vitro* incubation method (Bracher et al. 1999) were used. The range of daily areal production rates (ADP) were similar, but, at definite stations the variation was big (Table 4.2). Overall, only 8 stations were compared. The uncertainty of the results is probably due to differences between two different incubation methods. In the simulated *in situ* (SIS) method of Tremblay (1997) samples from 6 depths between surface and 0.1 % light depth were incubated 24 hours under natural light conditions on deck of the ship. In the *in vitro* (IV) method (Bracher et al. 1999) P versus E curves from surface and 1% light depth were performed in incubations over 4 hours under an artificial light source excluding UVR. Each P versus E curve contained 18 to 24 data points.

Table 4.2: Comparison of areal primary production rates (ADP) in [mg C m^{-2} d^{-1}] measured at various stations during the ANTXIII/2 cruise by two different methods: the simulated *in situ* (SIS) method was used by Tremblay (1997) and the *in vitro* (IV) method was used in our study (Bracher et al. 1999)

station	Tremblay (1997) SIS-method	Bracher et al. (1999) IV-method
9	440	172
13	1126	303
16	958	310
18	675	539
21	674	851
30	630	558
31	216	111
32	576	344

In the SIS-method UVR was included in the spectrum, but radiation within the bottles was 20 % higher in the PAR range, about the same in the UV-A range, and 50% lower in the UV-B range compared to the radiation at the sampled depth (unpubl. data). At several stations photoinhibition has been measured in surface water samples (Tremblay 1997). The cause of this photoinhibition might be either due to the naturally irradiances of UVR or due to an artefact by the unnaturally higher irradiances in the PAR range. In the Southern Ocean until now, photoinhibition has been reported only in SIS-incubations within polyethylene bags (Prezelin et al. 1994a, El-Sayed et al. 1990) or quartz bottles (Helbling et al. 1992) with significantly higher UVR transparency (75-

85%, Prezelin et al. 1994b), or in P versus E curves performed *in vitro* under simulated natural light conditions including UVR (Roettgers 1998). In contrast to that, in the IV-method UVR was excluded at all. In contrast to the rather blue colour encountered in the ocean, both incubation methods were performed under white light. Only the results of the IV-method were corrected by the *in situ* underwater light spectrum by correcting $\alpha_{\mathrm{incubation}}$ (*see* 4.4.1, Bracher et al. 1999), which is not possible to do for the SIS-method. With the IV-method it is possible to calculate areal daily primary production (ADP) rates until a depth, where no light during the daily cycle is measured at all; with the SIS-method ADP rates can only be calculated until the 0.1% depth. However, the comparison of ADP data until 0.1.% (between 50 and 100 m within the APFZ) and until 200 m depth showed that production below the 0.1% light level indeed makes only a negligible contribution to the complete vertically integrated production (Strass et al. 1999 - Table 4.3).

Table 4.3: Sensitivity of areal production rates to variation of the integration depth. The values indicate the average daily rates obtained from the whole survey period. within the APF and the SAPF during the ANT XIII-2 cruise. Table was taken from Table 2 in Strass et al. (1999)

integration depth	mean [mg C m^{-2} d^{-1}]	standard deviation [mg C m^{-2} d^{-1}]	range [mg C m^{-2} d^{-1}]
1 % light depth	554	± 164	268 - 924
0.1 % light depth	583	± 172	294 - 973
200 m	585	± 172	295 - 975

Short incubations (order of 1h) provide estimates that are closer to the gross carbon uptake than long incubations, because the likelihood of labelled carbon being respired to CO_2 and /or recycled within the cell increases with the duration of the incubation (Dring and Jewson 1982). In addition to that, it is recommended to keep incubation times as short as possible, since physiological acclimation of the photosynthetic apparatus to incubation conditions takes place, i.e. as a result of variations in light, temperature and nutrients (Sakshaug et al. 1997). Within 24 hour incubations, like it was done in the SIS-method, the physiological response of phytoplankton to the varying light field changes. This may be correct regarding differences in light intensity due to cloud cover, but not for the above mentioned qualitative differences to the *in situ* underwater light field. By contrast, the P versus E experiments in Bracher et al. (1999) were performed by shorter incubations (four hours). However, the constant incubation conditions when performing P versus E curves may bear an error when calculating ADP rates; although weaker developed in the Antarctic Ocean as compared to other regions, phytoplankton physiology responds to the diurnal light cycle (Rivkin and Putt 1988, *see* discussion in Bracher et al. 1999). At least, light values for calculating ADP rates included the day cycle of underwater irradiance by combining in-air-on-line measurements of PAR, E_a[PAR], the attenuation coefficient of PAR, k_d[PAR], and the conversion factor r from in-air-PAR to underwater-PAR, obtained with the MER light meter at all stations (Bracher et al. 1999, Strass et al. 1999).

In comparison to both methods, natural conditions would be best simulated by *in situ* incubations, but often, especially in the Southern Ocean due to the rough weather conditions, they are too laborious to conduct. Incubation bottles themselves affect the light climate during incubation. Quartz or certain polyethylene (which are much cheaper) bottles are the best to take because they are transparent to all spectral wavelengths; still only 80 % of the incoming light is let through (Prezelin et al. 1994b). No method includes the influence of algae wandering within the water column due to (vertical and horizontal) mixing on the ADP rate. Until now this phenomenon is still very poorly investigated. Depending on mixing rates and depths, ADP rates by static incubation are either under- or overestimated (Harris and Piccinin 1977, Marra 1978, Mitchell and Holm-Hansen 1991b, Helbling et al. 1994).

During ANT XIII/2 a 3-dimensional map of primary production at the Antarctic Polar Front was obtained by a diagnostic model which used on-line data (of light attenuation, global radiation, chlorophyll fluorescence), except for the parameters describing the P versus E curve, gathered within a small areal grid (Strass et al. 1999). In contrast to experimental primary production estimates based on a few single stations, the diagnostic model is able to yield a synoptic map which gives the high horizontal resolution required to seek a correlation with mesoscale hydrographic details, and to reveal temporal variations resulting from changes in global solar radiation. Consequently, based on adequately resolved variations in time and space, average primary production rates can be obtained which are less likely biased than experimentally derived values

(Strass et al. 1999 - Fig. 4.15). The effort to achieve this map of primary production was hardly bigger than for a few stations. Still it is questionable, if the values obtained by that model are of the same quality as direct measurements, since far more calibration and conversion steps were necessary. Light data were converted using spectrally resolved irradiance data of the stations, where also values of P^*_m and α^* were obtained at the stations. Station data have been sampled not during the fine-scale survey itself, but prior or afterwards. In addition to that, the diagnostic model did not incorporate UVR or photoinhibition into the analysis since, it was based on the IV incubations and the light meter on the undulating instrument did only measure PAR. This is a quick method to obtain a simultaneous picture of primary production rates on a high spatial resolution. In contrast to experimental estimates, those data can be compared to primary production estimates given by remote sensing on a high spatial resolution.

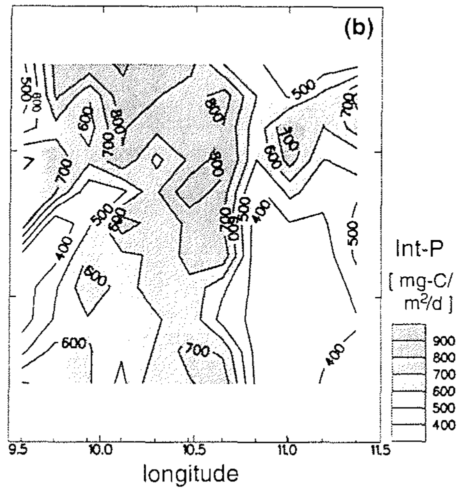

Fig. 4.15: Mean ADP rates of primary production integrated vertically to 200 m depth (b) within the APF and the SAPF during the ANT XIII-2 cruise. Figure was taken from Fig. 8b in Strass et al. (1999)

4.5 Application to remote sensing

4.5.1 Obtaining pigment concentration

Remote sensing by satellites promises to provide detailed synoptic information on phytoplankton biomass and productivity on a temporal and spatial scale. Satellites, however, depend on clear skies to get an image of the ocean colour. Thus, in the

Southern Ocean, where cloudy weather is prevailing, obtaining satellite data can be often severely restricted. Ocean colour data from the Southern Ocean have been gathered by the Coastal Zone Color Scanner (CZCS) on the Nimbus-7 satellite which was operational from 1978 to 1986 (Longhurst et al. 1995). Since October 1997 the Sea-viewing-Wide-Field-of-view-Sensor (SeaWiFS) on SeaStar satellite is working. The remote sensed signal is used to infer chlorophyll *a* concentration from measurements of light reflected from near surface waters. Increased absorption with increased biomass at the blue end of the spectra result in an increased reflectance in the green and decreased reflectance in the blue (Morel and Prieur 1977). This dependence of the spectrum of water leaving radiance on chl *a* + phaeo *a* is the basis of remote sensing algorithms for phytoplankton pigments. Most part of the world oceans, nearly the whole Southern Ocean, belong to the case I waters, being defined as waters whose optical properties almost entirely are determined by phytoplankton and its associated debris and breakdown products (Morel 1988). Gordon et al. (1983) developed a global-processing-algorithm (GP) for case I waters:

$$\log(\text{chl } a + \text{phaeo } a) = \log a + b \log R_i \qquad \text{(equation 4.1)}$$

$R_i = L_w[443] / L_w[550]$ for chl *a* + phaeo $a < 1.5$ mg m^{-3}

and $a = 0.14$, $b = -1.55$ $(r^2 = 0.97, n = 33)$

or $R_i = L_w[520] / L_w[550]$ for chl *a* + phaeo $a \geq 1.5$ mg m^{-3}

and $a = 0.63$, $b = -4.72$ $(r^2 = 33, n = 33)$

with L_w = radiance just above the surface measured by remote sensing

The reflectance data obtained by remote sensing can be compared to reflectance data measured underwater as upwelling radiance, L_u, (Austin 1980):

$$L_w \cdot 1.84 = L_u \qquad \text{(equation 4.2)}$$

One of the fundamental limitations of remotely sensed data on ocean colour is that information on the vertical structure of the pigment field, B(z) (with B =chl *a* + phaeo *a* at depth z), is lacking. It would not matter when B(z) were nearly uniform, but in many instances this is not the case. The existence of a peak in the profile, the deep chlorophyll maximum, is wide spread over much of the ocean (Cullen 1982, *see* chapter 3). Taking into account the vertical distribution of chlorophyll leads to small, but systematic differences in the calculated primary production (10% on basin scale, up to 20% at the province scale- according to Sathyendranath et al. 1995) compared with an approach that would assume a uniform chlorophyll distribution of magnitude equal to satellite derived value (Morel and Berthon 1989).

Table 4.4: Different parameters describing the algorithm, which converts R_i (=reflectance data from the ocean surface obtained by remote sensing) into chl *a* + phaeo *a* (=pigment concentrations). Parameters were derived by correlating [chl *a* + phaeo *a*], determined by various in situ studies at different locations, to R_i, by using the algorithm: log (chl *a* + phaeo *a*) = log a+ b log R_i; with $R_i = L_w [\lambda_1] / L_w [\lambda_2]$; with SO = Southern Ocean, ASO = Atlantic sector of Southern Ocean, and BASO = bloom within Atlantic sector of Southern Ocean; * = in these studies reflectance data were derived by using upwelling radiation, measured with an underwater spectrometer

L_w [441] / L_w [550]

citation	Gordon et al. 1983	Mitchell and Holm-Hansen 1991*	our study *	our study *
where	global	SO	ASO	BASO
N	33	122	13	10
r_2	0.97	0.83	0.53	0.54
a	0.14	0.53	0.12	0.19
b	1.55	1.63	-1.12	-0.55
a+c.l.		0.32	0.07	0.04
b+c.l.		0.12	0.54	0.30

L_w [520] / L_w [550]

citation	Gordon et al. 1983	Mitchell and Holm-Hansen 1991*	our study *	our study *
where	global	SO	ASO	BASO
N	33	122	13	10
r_2			0.81	0.97
a	0.63	0.48	0.27	0.27
b	4.72	3.32	-5.23	-3.21
a+c.l.		0.38	0.07	0.02
b+c.l.		0.38	1.14	0.30

Mitchell and Holm-Hansen (1991a), have developed a Southern-Ocean-algorithm (SO) using a large data set of pigment and reflectance data from the area of the Drake Passage to the Antarctic Peninsula, since their results obtained by the GP algorithm were significantly different (Table 4.4). In accordance to them, we used our surface chl *a* + phaeo *a* and R_i data of the second JGOFS cruise (Bracher and Tilzer 1999) for linear regression and developed separate algorithms for R_i = L_u[443] / L_u[550] and R_i =

$L_u[520]$ / $L_u[550]$. For the stations in the bloom areas (>1 mg chl *a* m^{-3}) we developed a bloom algorithm (Table 4.4). We only had R_i data for three stations outside the bloom, therefore no separate algorithm for those stations could be developed. Linear regression for $R_i = L_u[520] / L_u[550]$ data gave much better correlation to chl *a* + phaeo *a* with r = 0.81 (bloom 0.97) as opposed to $R_i = L_u[443] / L_u[550]$ with 0.53 (bloom 0.54), (Fig. 4.16).

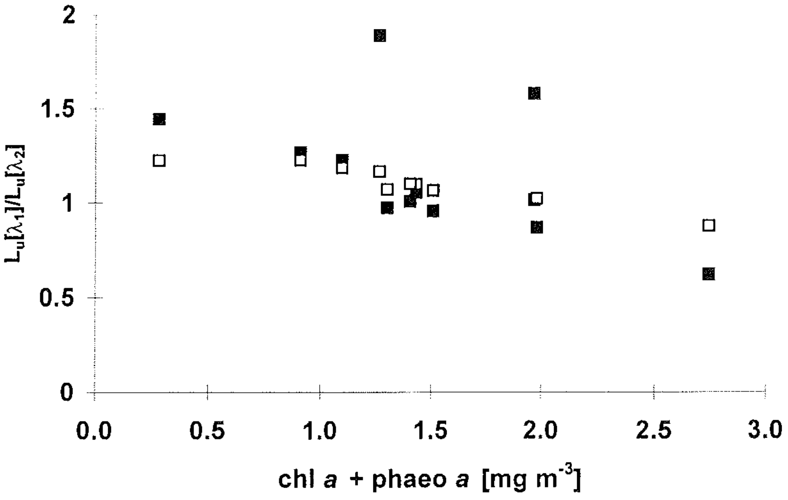

Fig. 4.16: The reflectance data, R_i, measured by the underwater spectrometer MER 2040 as upwelling radiance, $L_u[\lambda]$, as a function of surface chlorophyll *a* and phaeophytin *a* concentration (chl *a* + phaeo *a*) during ANT XIII/2 cruise (publication I). Black points mark reflectance data with $R_i = L_u[443] / L_u[550]$ and white points mark $R_i = L_u[520] / L_u[550]$

We compared calculated chl *a* + phaeo *a* concentrations by using our R_i data and the GP, SO and our own algorithms, to the *in situ* measured chlorophyll concentrations (Fig. 4.17). Our algorithm (with $R_i = L_u$ [520] / L_u [550]), gave the far best estimate for chlorophyll concentrations. The SO and the GP algorithms overestimate pigment concentration significantly by >150% (± 151%) and >50% (±84%), respectively. For lower biomass (<1.5 mg chl *a* m^{-3}) the GP algorithm was even better than the SO algorithm, but, for high biomass the SO algorithm was better. Using our total algorithm standard deviation is still high with 47%, while the bloom algorithm shows only 8%.

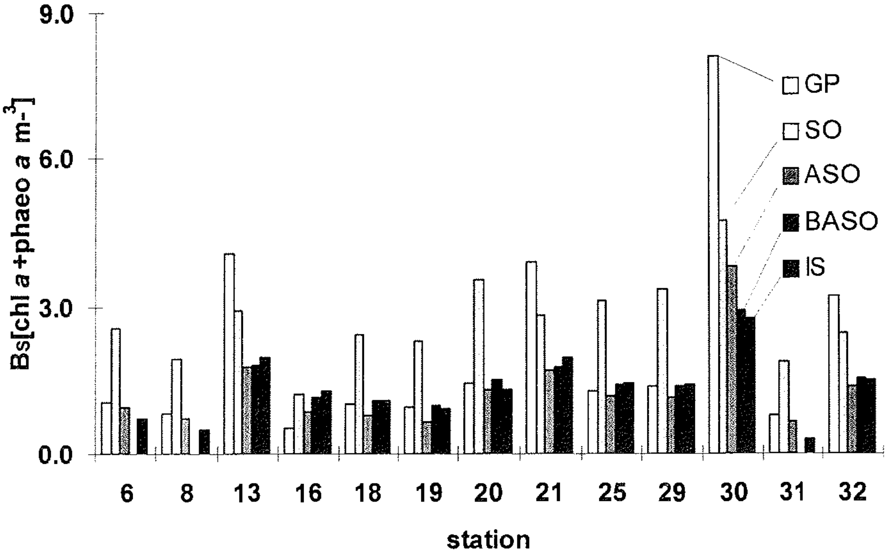

Fig. 4.17: Data of chlorophyll *a* and phaeophytin *a* concentration at the surface, B_s, measured *in situ* (= IS) and calculated according to various algorithms (parameters *see* Table 4.2): by GP = according to the global-processing-algorithm developed by Gordon et al. (1983), the SO = the Southern-Ocean-algorithm developed by Mitchell and Holm-Hansen (1991), the ASO = the Atlantic-Southern-Ocean-algorithm developed in this study with *in situ* upwelling data, and the BASO = the Atlantic-Southern-Ocean-algorithm at phytoplankton blooms developed in our study with *in situ* upwelling data from stations with $B_s > 1$ mg m^{-3}

Regional and seasonal variations in the environment lead to significantly different biooptical properties of particulates (e.g. Mitchell and Kiefer 1988, Mitchell and Holm-Hansen 1991a, Lutz et al. 1995, Sathyendranath et al. 1996, Bracher and Tilzer 1999 and Bracher et al. 1999). Pigment specific inherent optical properties and apparent optical properties may result in different relationships between $L_u[\lambda]$ and chl *a* + phaeo *a* (Morel 1988). Our results manifest when using remotely sensed ocean colour data to convert into pigment concentrations not only an algorithm specific for the Southern Ocean has to be developed as claimed by Mitchell and Holm-Hansen (1991a) and

Mitchell (1992), but also different algorithms for the biogeochemical provinces within this ocean. When blooms are encountered at the APF or south by a decrease in the ratio of reflectance at 520 nm to 550 nm, one can be sure that they are formed by netplankton. In addition, at blooms of very shallow UMLs (<20 m) often phytoplankton below the UML show low light adaptation which results in a vertical change of a_ϕ*. Depending on the attenuation length this can still affect the reflectance signal. Therefore, for estimating chlorophyll concentrations a different algorithm has to be used than for the rest of the Southern Ocean. Otherwise those values will be underestimated within blooms.

4.5.2 Obtaining primary production rates

At present, remote sensing does not provide a direct measure of primary productivity; this must be inferred from the relationship between primary productivity and chlorophyll *a* concentration. For estimating local marine primary production in the ocean, several procedures are available using light-dependent models of photosynthesis, which require the following information: the sub-surface light field just below the sea surface (E_0), as a function of time; the distribution of diffuse attenuation coefficient for downwelling light (k_d) and the chlorophyll (B) with depth (z) in the water column; and finally as a function of depth, the parameters of the P versus E curve: α^*, P^*_m (Sathyendranath and Platt 1993). In addition, also the parameter characterising photoinhibition might be necessary β^*.

Any computation of primary production at large scales requires information, but resolved appropriately in space and time. Satellite provides some, but not all, of the required information with appropriate spatial and temporal resolutions: thus, cloud fields can be combined with atmospheric transmission models to obtain E_0 (Bishop and Rossow 1991); sea surface colour fields contain information on near-surface pigment concentration B_s, and since B(z) and $k_d(z)$ are closely related, at least in open ocean waters, we can also infer something about k_d (Gordon and Morel 1983, Sathyendranath and Morel 1983). But satellite remote sensing provides neither depth resolved B or k_d, nor the P versus E parameters. Therefore, large scale computations of primary production must be approached by combining satellite and *in situ* observations, and this requires techniques for extrapolating *in situ* observations in space and time, to match satellite data base. The relevant properties to be extrapolated are the parameters that define the shape of the chlorophyll profile (and therefore B and k_d), and the P versus E parameters. According to Platt and Sathyendranath (1988) and Sathyendranath et al. (1995) this spatial discontinuity in biooptical characteristics should be recognised not only for conversion of reflectance data into pigment concentration, but also when deriving primary productivity from these values.

Sathyendranath et al. (1995) portioned the North Atlantic into biogeochemical provinces. The ocean was partitioned, in addition to relying on oceanographic intuition, by taking into consideration more than 6000 chlorophyll profiles, parameterised for their shape according to a standard equation (shifted Gaussian), and nearly 2000 sets of photosynthesis parameters from this part of the world. By this procedure, the ocean was divided into a set of biogeochemical provinces whose nominal boundaries, as well as being plausible to oceanographic insight, were also consistent with the observed patterns, considered seasonally in their data base. Biooptical information of our study within the area around the polar front will probably be sufficient to be used, in addition to information obtained by remote sensing, for deriving primary production rates at this time of the year (early summer). Here data acquisition of underwater light, chlorophyll fluorescence and CTD-parameters within the water column were obtained on-line, P versus E parameters were measured at numerous points within this area and extrapolated due to correlation with mesoscale hydrographic details (Strass et al. 1999). At other sites of our study within the Southern Ocean the information on biooptics was not obtained in this dense resolution, and therefore, before they can be extrapolated in a similar way like it was done in Strass et al. (1999) or described by Sathyendranath et al. (1995), additional data acquisition is necessary.

4.6 Concluding remarks and future perspectives

It is concluded from this thesis that biooptical characteristics, phytoplankton production, biomass and composition of phytoplankton within the Southern Ocean, are showing regional differences which are reflected in different biogeochemical provinces. In areas of enhanced biomass and primary productivity within the Southern Ocean phytoplankton are comprised mainly of net-plankton (>20 µm), mostly dominated by diatoms. Only the second period of blooms within the MIZ and in coastal waters can be dominated by big colonies of *Phaeocystis*. The frontal regions north of the APF (within the STC and the SAF) mainly consist of nanoplankton. By contrast, interfrontal areas year round are characterised by scarce phytoplankton biomass, low primary productivity and pico- and nanoplanktonic flagellates belonging to various algal classes.

The observed distribution of phytoplankton community composition is governed by a complex of inter-dependent factors which are the result of phytoplankton growth and loss factors. Phytoplankton blooms within the Southern Ocean are spatially and temporally restricted in their occurrence and mainly occur on sites where a shallow upper mixed layer (at least <50 m) has been established; still substantial biomass may extend to depths below the shallow UMLs, where growth rates are light-limited. This may be a result of hydrodynamically caused subduction of the surface waters where bloom formation had been facilitated earlier under favourable light conditions as a consequence of shallow mixed layer depths. In addition, phytoplankton growth may be restricted by temperature and iron availability, while only at the northern boundary of the APF silicate concentrations may limit phytoplankton (mainly diatom) growth. Grazing influences biomass build-up and the distribution of size fractions within phytoplankton communities. The understanding of the regulation of phytoplankton productivity and biomass in the Southern Ocean is crucial for the understanding on effects of global climate change by radiative forcing (enhanced UV radiation, heating, melting of pole caps, and CO_2 concentrations in the atmosphere) to the ocean's food web structures and carbon fluxes.

Effects of enhanced levels of UVR caused by stratospheric ozone depletion seems to impair primary production in the Southern Ocean stronger outside of phytoplankton blooms than within. Within blooms protection by MAAs acting as sunscreens is much more efficient because the phytoplankton community is mainly comprised of the fraction of cells, colonies or chains >20µm. Since smaller phytoplankton (<10 µm) and phytoplankton under unstable hydrological conditions are more susceptible to UVR damage, during austral spring the increasing UV-B radiation due to changed ozone levels in the stratosphere might delay the initiation of a bloom and alter species composition in the Southern Ocean. Thereby both the marine food web and the global carbon fluxes will be affected.

To extrapolate our findings to a global-scale feature, phytoplankton productivity can be estimated on the basis of remotely sensed chl *a* concentrations provided that temporal and spatial resolution is sufficient. Photoacclimation and cell size are determining pigment packaging and backscattering. Spectral light absorption characteristics are pigment specific. Hence, variations in all above mentioned parameters lead to differences in pigment specific inherent (e. g. $a^*[\lambda]$) and apparent optical properties (e. g. $k_c[\lambda]$), which affect the underwater light field. Thus, also the reflectance signal obtained by remote sensing is influenced. Since those biooptical parameters differ between the phytoplankton communities of the different biogeochemical provinces in the Southern Ocean, algorithms used for deriving correct pigment concentrations from remotely sensed reflectance data should not only be specific for the Southern Ocean as a whole, but also should be specific for the various biogeochemical provinces. This conclusion is supported by the comparison of *in situ* upwelling data and chlorophyll concentrations measured during our survey.

However, satellites depend on clear skies to obtain an image of the ocean. This represents a major problem in the Southern Ocean with prevailing cloudy weather. Moreover, remote sensing does neither provide information of vertical phytoplankton distribution, the underwater light field, nor the P versus E characteristics. Therefore, large - scale computations of primary production must be based on the combination of satellite and *in situ* observations, and this requires techniques for extrapolating *in situ* observations in space and time, to match the satellite data base. By on-line mapping, an array of relevant parameters can be obtained in a quasi-synoptic fashion over the vertical profile: temperature distribution, current patterns, flow patterns, underwater light field and chlorophyll concentration by using an instrument package comprising a shipboard - based Acoustic Doppler Current Profiler and a towed undulating vehicle (e.g. SeaSoar) housing sensors for temperature, conductivity, pressure, PAR and chlorophyll fluorescence (instrument description *see* Pollard et al. 1995). We used such a device for obtaining input variables for our model resolving the spatial distribution of primary production at the APF. To obtain time series of data at one site, the instruments can be mounted on a platform suspended by buoys. In addition, *in situ*-multiwavelength-transmissiometers suspended from such buoys deliver time - series information on phytoplankton composition based on pigment composition (Johnsen 1994). Our data showed that differences in biooptical parameters due to species composition and photoacclimation among the biogeochemical provinces affect calculations of primary production by relating chlorophyll concentrations to underwater irradiance. When using our information on P versus E parameters and phytoplankton absorbance for deriving primary productivity, the spatial heterogenity in biooptical characteristics, as obtained by the conversion of reflectance data into pigment concentration, also has to be considered.

Between October and December, the effect of enhanced UVR due to ozone depletion has to be taken into account when estimating primary production rates. Consequently, assessments of P versus E curves should be conducted by using a sunshine simulator, used in Bracher and Wiencke (1999), under irradiance conditions responding to ozone layer concentrations measured in this area, in order to obtain the inhibition term β^* which has to be used in algorithms to. Information on stratospheric ozone layer concentrations above a certain area can be obtained daily from data derived by Tiros Operational Vertical Sounder (TOVS) aboard the NOAA polar orbiter. If primary production is estimated in the Southern Ocean at areas outside of blooms, the P versus E parameters charcteristic under this spectrum have to be taken into account, according to the TOVS data measured at that time and that place.

A future approach to estimate the photosynthetic parameters will be utilising environmental proxies, especially those which are accessible by remote sensing. But, for developing such an estimation procedure, one requires a body of data as a starting point. Knowledge of the initial slope of the light saturation curve as well as the assimilation number is inevitable, and until the insight to construct an estimation procedure for them, the main task is to extend their empirical data base. New techniques for measuring P versus E parameters in natural sea-water samples are developed: fast-repetition-rate-fluorometer (FRRF), the-pump-and-probe-fluorometer (PPF) and the pulse-amplitude-modulated-fluorometer (PAM) (for further details *see*: Falkowski and Kolber 1993, Schreiber et al. 1995). When these techniques, which are fast and non-destructive, will be proven to be robust, and can be mounted on an undulating platform or towed instrument (e.g. SeaSoar), both vertical and horizontal profiling will be possible. Then, a great step towards filling the gaps in our knowledge of the distribution of the P versus E parameters in nature can be made. In addition, also sensors spectrally resolving the underwater light field including UVR should be mounted on an platform or a towed instrument.

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