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Phaeocystis antarctica Karsten as an Indicator Species of Environmental Changes in the Antarctic

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ABSTRACT. *Phaeocystis antarctica* Karsten is widely distributed in Antarctic waters, and forms massive near-surface blooms in the marginal ice-edge zone. Because of the location and timing of the *P. antarctica* bloom, this prymnesiophyte has been exposed to high levels of UV-B (280 to 320 nm) radiation. UV-B-induced changes in species composition favouring the colonial stage of *P. antarctica* would be the potential for altered trophodynamics and carbon flux in Antarctic waters as a result of ozone depletion. The overall physiological impact of increased UV-B exposure on *P. antarctica* would presumably shift the balance between photosynthesis and respiration, resulting in consequent changes in species composition. In this paper, we briefly review *P. antarcitca*-dominated ecosystem in the Antarctic, taxonomic identity and life cycle of *P. antarctica*, microbial degradation of *P. antarctica* material in the water column, sedimentation and regeneration of *P. antarctica* blooms, and the trophic significance of *P. antarctica* blooms. Then we review dimethyl sulfide (DMS) and *P. antarctica*, response of *P. antarctica* to UV-B fluctuations. The observed long-term increase of *Phaeocystis* bloom occurrences in the Antarctic waters gives support of the good adaptability of colony forms to growth in the changing environment, rendering *Phaeocystis* appears to be useful as indicator species of long-term and/or chronic environmental changes, such as climate and environmental changes (e.g. eutrophication, UV-B effects, global warming).

Key Words: DMS, environemtal change, indicator speices, Phaeocystis antarctica, UV-B

Introduction

Prymnesiophyte *Phaeocystis* Lagerheim is one of the most widespread marine genera. *Phaeocystis* is very unique in that it exhibits phase alternation between free-living cells (flagellates = zoids) of 3-9 μm in diameter and gelatinous or mucilaginous colonies of non-motile coccoid cells (palmelloid stage, vegetative cells) reaching several mm; its complex polymorphic life cycle and associated physiology induces dramatic structural changes in the ecosystems (Lancelot *et al.* 1994). No other marine phytoplankton has ever been shown to dominate an entire ecosystem. No other marine species distinguishes itself by a complex polymorphic life cycle that induces dramatic changes in the structure and functioning of the planktonic and benthic food-web as well as in the biogeochemistry of trace elements and sulfur (Rousseau *et al.* 1994).

Phaeocystis blooms are reported from a wide variety of ecosystems; such as areas with (a) high nutrient concentrations and high mixing (the North Sea; Eberlein *et al.* 1985), (b) weak stratification and mesotrophy (the Barents Sea and Norwegian fjords; Estep *et al.* 1990; Passow and Wassmann 1994), (c) strong stratification and high nutrient concentrations (marginal ice-edge zones; Garrison *et al.* 1987; Smith 1991).

Phytoplankton populations in the Antarctic have been found to be dominated by *Phaeocystis antarctica* Karsten in colonial stage, which has been reported

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from the Weddell Sea (Buck and Garrison 1983; Garrison and Buck 1985; Garrison *et al.* 1987; Fryxell and Kendrick 1988; Fryxell 1989; Kang and Fryxell 1993; Kang *et al.* 1995), the Ross Sea (El-Sayed *et al.* 1983; Palmisano and Sullivan, 1983; Palmisano *et al.* 1986; Knox 1990; DiTullio and Smith 1996), the Bellingshausen Sea (Bidigare *et al.* 1996), and the Prydz Bay (Perrin and Marchant 1987; Davidson and Marchant 1992).

The overall objectives of this paper are to review key phytoplankton species in the *Phaeocystis antarcitca*-dominated ecosystem in the Antarctic and have information on the dominant phytoplankton species to be used as an indicator species of long-term environmental changes such as UVR increase and global warming. The specific objectives of this paper are to review (1) ecology of *P. antarctica*-dominated ecosystems; (2) taxonomic identity of *P. antarctica* ; (3) life cycle of *P. antarctica*; (4) microbial degradation of *P. antarctica* material in the water column; (5) Sedimentation and regeneration of *P. antarctica* blooms; (6) The trophic significance of *P. antarctica* blooms; (7) Dimethyl sulfide (DMS) and *P. antarctica*; (8) Response of *P. antarctica* to UV-B fluctuations

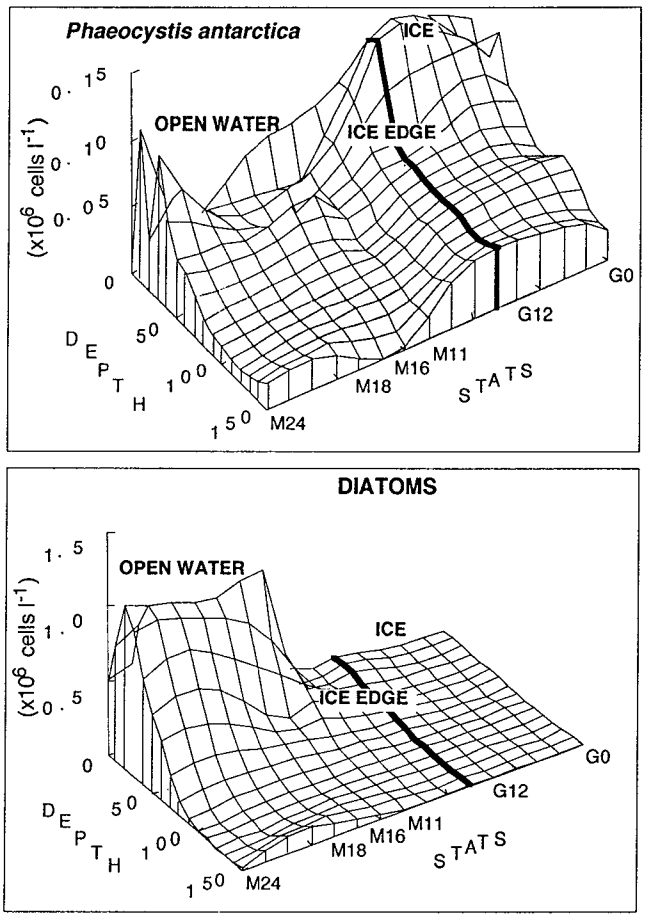

Fig. 1. Coparison of distributional patterns of *Phaeocystis antarctica* and diatoms in the upper 150 m along a transect near marginal ice-edge zone of Weddell Sea (from Kang and Fryxell 1993).

Ecology of *Phaeocystis antarctica*-Dominated Ecosystems

Kang and Fryxell (1993), Kang *et al.* (1995), and Bidigare *et al.* (1996) reported variations in abundance and distribution of the *Phaeocystis antarctica* and diatoms in spring and autumn in the Weddell Sea (Fig. 1) and in the Bellingshausen Sea (Fig. 2) that apparently were related to the gradient in environmental condition across the ice-edge zone. Few reports have addressed the spatial variations of *P. antarctica* abundance and biomass across the marginal ice-edge zone (MIZ) in both horizontal and vertical dimensions. There are still many open problems concerning the mesoscale distributions of Antarctic phytoplankton due to existence of localized mechanisms of phytoplankton enrichment. It is essential to quantify dominant phytoplankton species at certain time and location and elucidate major factors affecting structure of phytoplankton assemblages. Field studies conducted under the influence of various physicochemical properties of the surrounding water can provide in situ data set required to quantify the dominant phytoplankton species and to elucidate the factors influencing structure of phytoplankton assemblages.

Initiation of *Phaeocystis antarctica* bloom was determined by physical processes. The physical processes associated with ice retreat enhance the development of *P. antarctica* blooms at the receding ice-edge by providing phytoplankton cells with optimal light conditions owing to the formation of shallow vertically stable surface layer as a result of meltwater production (Smith and Nelson 1985, 1986; Sullivan *et al.* 1988; Comiso *et al.* 1990).

Magnitude of the *Phaeocystis antarctica* bloom at the MIZ is regulated by vertical stability of surface

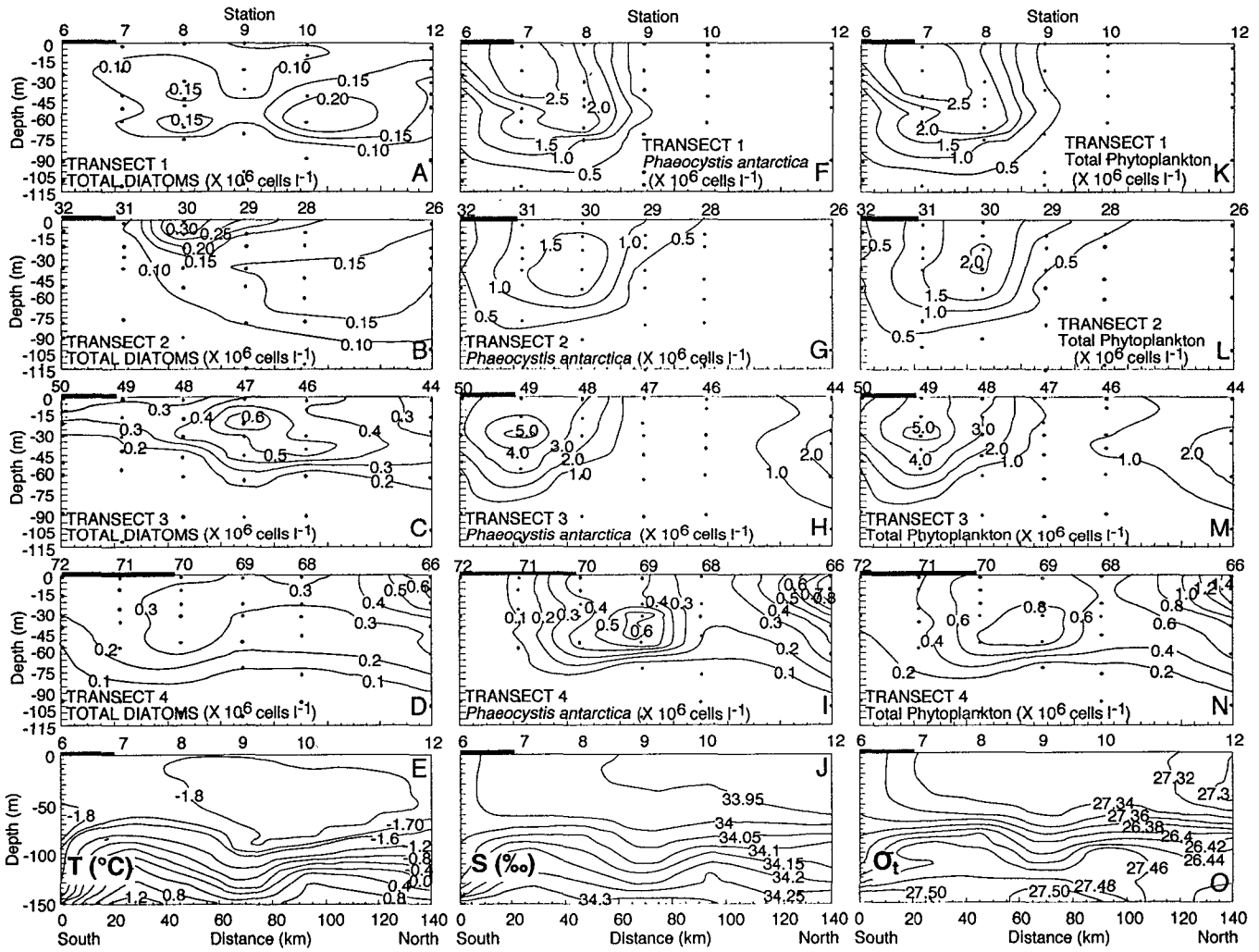

Fig. 2. Contour plots of diatoms, *Phaeocystis antarctica*, and total phytoplankton cell abundance in the upper 115 m along transects near marginal ice-edge zone of Bellingshausen Sea during Icecolors 90 (from Bidigare *et al.* 1996).

waters. Rapid degradation of the meltwater lens at its seaward edge by deep vertical lens due to violent winds prevailing in this extreme environment prevents *P. antarctica* cells from growing under optimal light conditions (Holm-Hansen *et al.* 1977; Smith and Nelson 1985; Sullivan *et al.* 1988). Thus, the magnitude of *P. antarctica* bloom depends on the persistence of the vertical stablity. Wind mixing events - their duration, strength, and frequency - determine both the distance from the ice-edge of the sea ice associated *P. antarctica* bloom and occurrence in the ice-free area of secondary *P. antarctica* blooms during the summer period.

Phaeocystis antarctica (colonial stage) was a significant biomass source due to their high numerical abundance (Fryxell and Kendrick 1988; Kang and Fryxell 1993; Kang *et al.* 1995). Integrated *Phaeocystis* carbon in the upper 100 m of the water column ranged from 5.1 to 7.6 g C m^{-2}. Although larger-celled diatom species were considered important biomass source due to their large cell volumes in other ice-edge zones, *P. antarctica* (colonial stage) appeared to out-compete the larger-celled diatoms in the MIZ.

Davidson and Marchant (1992) found that *Phaeocystis antarctica* was the first major phytoplankton species to bloom, reaching concentrations of 6 x 10^7 cells/l and remained numerically dominant for most of the summer in the Prydz Bay. During the *P. antarctica* bloom the concentration of most other autotrophs did not increase. Microheterotroph abundance peaked during or immediately after the *Phaeocystis* bloom. In the Weddell Sea ice-edge zone the richest phytoplankton areas (7.9-14.4 g C m^{-2})

were found associated with increased number of *P. antarctica* in colonial form (Kang *et al.* 1995). The colonial *P. antarctica* dominated phytoplankton stocks, reaching biomass of 7.6 g C m^{-2}, and average integrated biomass (3.0 g C m^{-2}) of *P. antarctica* was about 51 % of total phytoplankton carbon biomass.

In the northwestern Weddell Sea the relative abundance of *Phaeocystis antarctica* was high at ice-covered stations (> 60%) and low at open-water stations (< 16%). Waters in the Bransfield Strait region were characterized by a dominance of nanoflagellates such as *Cryptomonas* sp. and *P. antarctica* (motile stage), accounting for 83% of the total phytoplankton carbon (Kang and Fryxell 1993; Kang and Lee 1995).

Marine snow collected near Showa Station consisted principally of mucilage of colonial *Phaeocystis antarctica* derived from the sea-ice community. The abundance of polysaccharide-containing particles indicated an increase in the abundance of large colonies of *P. antarctica* (Marchant *et al.* 1996)

The Antarctic ice edge acts as a dynamic frontal system on the phytoplankton in the water column. In the Weddell Sea during spring in the open ocean near the marginal ice zone, long chains of vegetative cells with large vacuoles and gelatinous colonies of diatoms such as *Thalassiosira gravida* and of *P. antarctica* dominated (Fryxell 1989). In the northwestern Weddell Sea and eastern Scotia Sea the dominant taxa under the ice and in the ice-melt stations were the pennate diatom genus *Fragilariopsis* and *Phaeocystis antarctica* (Fryxell and Kendrick 1988). In the open ocean, the dominants were the centric diatom *T. gravida* and *P. antarctica*; both grew in gelatinous colonies, a growth habit that apparently gave competitive advantage and may have inhibited grazing. *P. antarctica* could have been seeded from the melting ice and from the water under the ice (Garrison *et al.* 1987).

The Taxonomic Identity of *Phaeocystis antarctica*

Sournia (1988) outlined diagnostic features of *Phaeocystis* species at the various life stages and pointed out the difficulty of identification of *Phaeocystis* species at the species level because of (1) the existence of poorly described taxa, (2) the alternation of different stages in the life cycles, and (3) practical difficulties of observation at the ultra-structural level. Although *P. pouchetii* (Hariot) Lagerheim has been considered as important Antarctic species and has been well described under both the motile and non-motile stages in previous studies (e.g. Davidson and Marchant 1992), Medlin *et al.* (1994) have found morphological, physiological, and genetic differences between *P. pouchetii* and *P. antarctica* from Antarctic waters.

Table 1. Colony morphology and temperature tolerance of *Phaeocystis antarctica* after Baumann *et al.* (1994a).

Criteria	Features
Colony morphology:	
- Maximum size	at least 9 mm
- Shape	spherical and numerous derived forms
- Cell distribution	evenly along the periphery
- Mucilage	solid
Physiology:	
- Growth range	-1.6 to 14°C
- Growth optimum	4.5°C (Fig. 3)
- Temperature tolerance	< -2 to 14°C

Phaeocystis species diversity has been reviewed by Baumann *et al.* (1994a) to compare the morphological and physiological characteristics of *Phaeocystis* cells and colonies of different geographical origin. Their analyses gave evidence that *Phaeocystis antarctica* was distinguished to other *Phaeocystis* species such *as P. globosa, P. scrobiculata,* and *P. pouchetii* in morphological characteristics (different palmelloid stages, e.g. shape and size of colony and single cell, organisation of the cells inside the colonies, thread-like appendages of the motile single cell, organic scales covering the cells, the haptonema and the flagella) and variation in temperature and light requirements and tolerance (Tables 1 and 2; Fig. 3).

There are distinct genetic differences between *Phaeocystis* species from different geographic areas

Table 2. Features of the motile cell of *Phaeocystis antarctica* after Baumann *et al.* (1994a).

Criteria	Features
Size	3-8 µm
Threads	pentagonal figure (length: 46 µm, diam. 0.1 µm)
Scales	Two different scale types present, but not characterized
Flagella	c. 12 µm long
Haptonema	not investigated

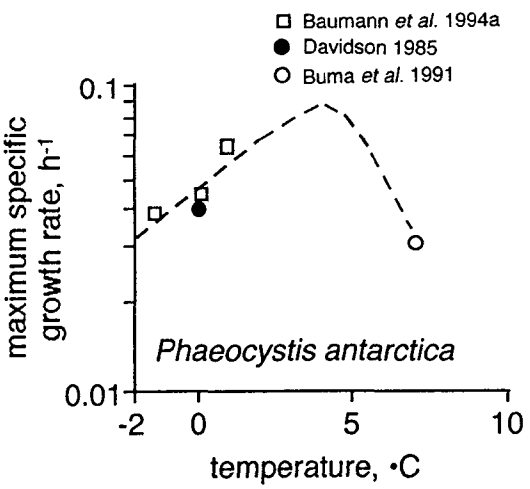

Fig. 3. Maximum specific growth rate of *Phaeocystis antarctica* versus temperature (from Baumann *et al.* 1994a)

even though cells are morphologically similar (Medlin *et al.* 1994). Until molecular characterizations were done by Medlin *et al.* (1994), Antarctic *Phaeocystis* species was called *P. pouchetii* or *Phaeocystis* sp. The most common epithet for Antarctic forms is *P. pouchetii* which was considered as Antarctic species: however, the cells observed in the Antarctic waters were most likely *P. antarctica* (Medlin *et al.* 1994).

Medlin *et al.* (1994) used sequence data from the 18S small subunit ribosomal RNA gene to differentiate the species status of three colony-forming species of *Phaeocystis*. *Phaeocystis antarctica*, described by Karsten (1905), was genetically different from *P. globosa* Scherffel and *P. pouchetii*. Morphological and physiological data were compiled from the literature to support the separation of the three species. Vaulot *et al.* (1994) examined cell (single and colony) morphology (colony formation and morphology, five-rayed star-like structures with filaments), cell size, ploidy level (haploid linked to flagellates and diploid linked to colonies), pigment composition (fucoxanthin, 19'-hexanoyloxyfucoxanthin, and diadinoxanthin), and genome size of *Phaeocystis*. Cell size was not a good criterion for distinguishing species since size distributions overlapped. On the basis of both pigment composition and genome size, the Antarctic species (*P. antarctica*) was different from others. Vaulot *et al.* (1994) concluded that the taxonomy of the genus *Phaeocystis* needs to be clarified through a combination of morphological, biochemical, and molecular studies.

The Life Cycle of *Phaeocystis antarctica*

Rousseau *et al.* (1994) reviewed the literature related to the life cycle of the prymnesiophyte *Phaeocystis* and its controlling factors. *Phaeocystis* exhibits a complex alternation between several types of free-living cells (non-motile, flagellates, microzoospores and possibly macrozoospores) identified on the basis of combination of size, motility and ploidy characteristics and colonies. Within *Phaeocystis* life cycle colony formation is not completely understood. Rousseau *et al.* (1994) observed that *Phaeocystis* colonies were initiated at the early stage of their bloom each by one free-living cell. The observation of haploid microzoospores released from senescent colonies supported to sexuality involvement at some stages of colony formation. Once colonies are formed, at least two mechanisms were identified as responsible of the spreading of colony form: colony multiplication by colonial division or budding and induction of new colony from colonial cells released in the external medium after colony disruption (Fig. 4).

Phaeocystis antarctica has been observed a complex alternation between several types of free-living cells (non-motile, flagellates, microzoospores, and possibly macrozoospores) and colonies for which neither forms nor pathways have been completely identified and described (Baumann *et al.* 1994a; Medlin *et*

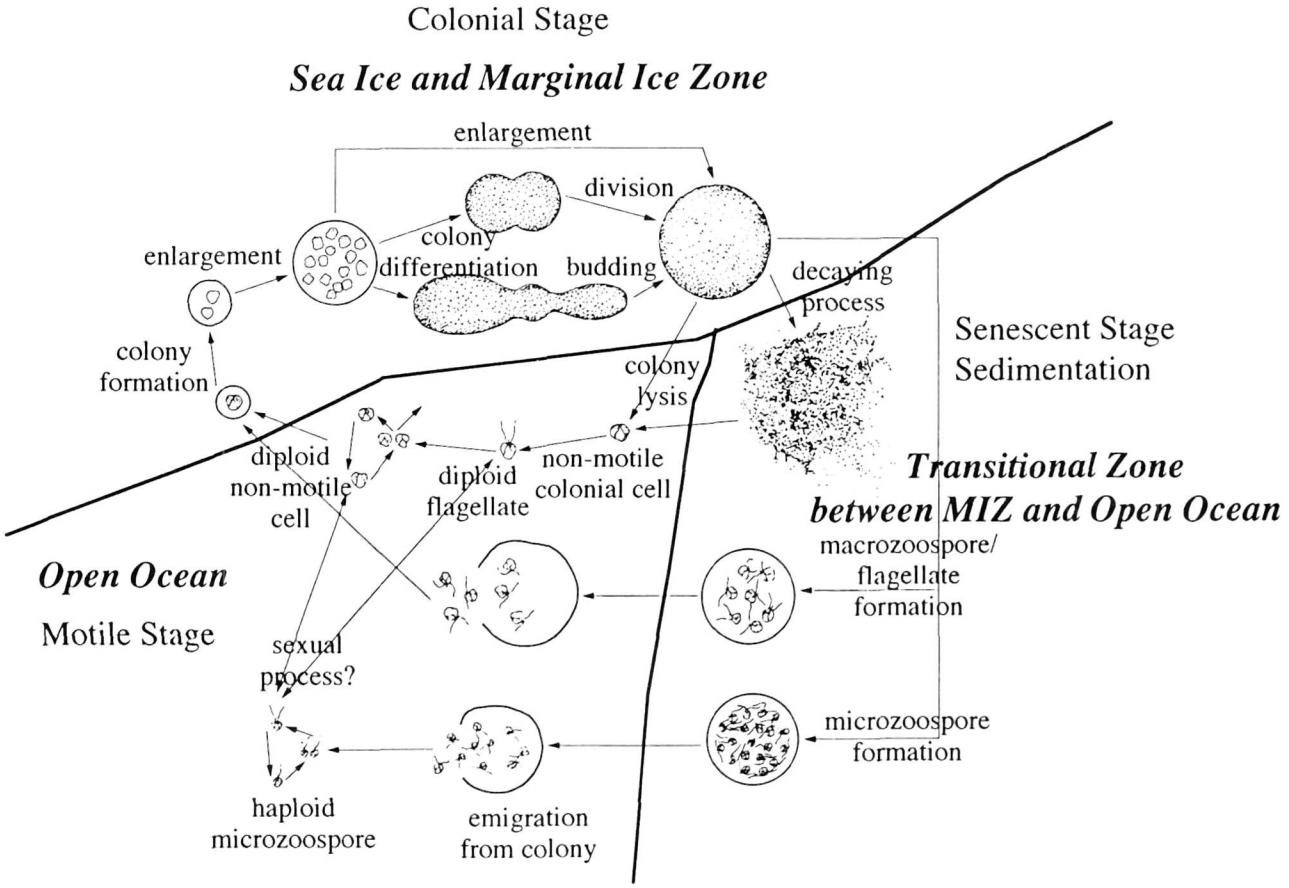

Fig. 4. Hypothetical life cycle of *Phaeocystis antarctica* redrawn from *P. globosa* life cycle as compiled from culture and field observation by Rousseau *et al.* (1994).

al. 1994; Vaulet *et al.* 1994). At least three different types of free-living cells identified on the basis of a combination of size, motility, and ploidy characteristics: 1) non-motile cells, 2) flagellates, and 3) microzoospores. Their respective function within *Phaeocystis* life cycle, and in particular their involvement in colony formation is not completely understood. Based on the hypothetical life cycle of *P. globosa* Scherffel from culture and field observation by Rousseau *et al.* (1994) we have redrawn speculated life cycle of *P. antarctica* based on field observation in the Weddell Sea ice-edge zones (Kang and Fryxell 1993; Kang *et al.* 1995; Kang and Lee 1995) (Fig. 4).

Colonial stage

Colonial cells are non-motile cells which size ranges between 4.5 and 8 μm (Fig. 5A, B). They have two or four chloroplasts and contain a vesicle of chrysolaminarin. They are deprived of flagella and haptonema, possess a longitudinal groove, lack the organic scales covering microzoospores and are surrounded by a mucilage envelope composed of about 10 layers roughly 0.5 μm wide (Rousseau *et al.* 1994). Once colonies are formed, at least two mechanisms were identified as responsible of the spreading of colony form: 1) colony multiplication by colonial division or 2) budding and induction of new colony from colonial cells released in the external medium after colony disruption (Fig. 4). The latter mechanism was clearly identified, involving at least two successive cell differentiation in the following sequence: motility development, subsequent flagella loss and settlement to a surface, mucus secretion and colony formation, colonial cell division and colony growth.

Aggregate formation, cell motility development (flagellates) and subsequent emigration from the colonies, release of non-motile cells after colony lysis were identified as characteristic for termination of *Phaeocystis* colony development wide (Rousseau *et al.* 1994). In the early stages of the bloom, many

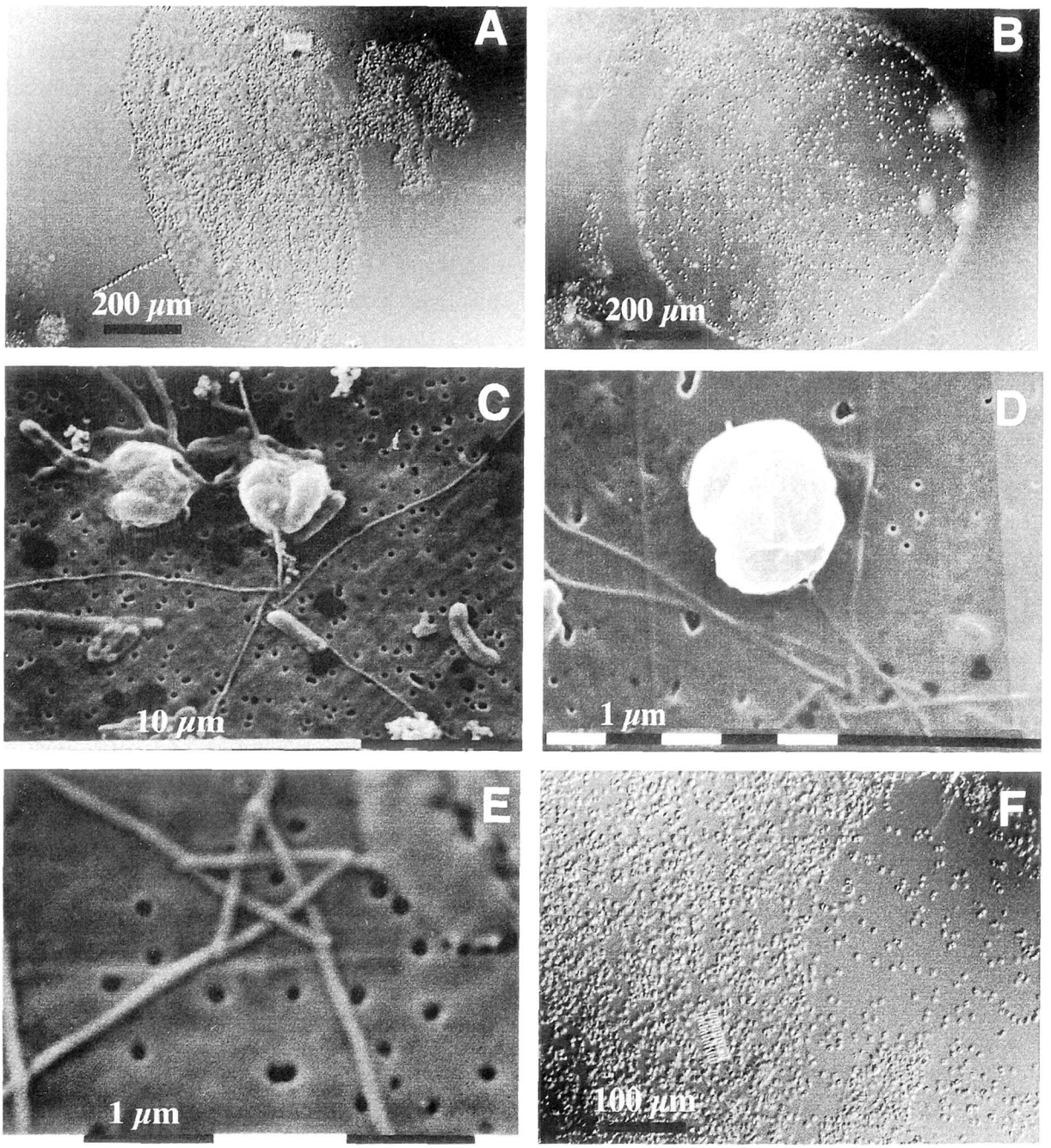

Fig. 5. *Phaeocystis antarctica* in varying stages of colony development from flagellate swarmers to *Phaocystis antarctica* cells in gelatinous matrix from Weddell Sea ice-edge zone during the 7th KARP cruise (1994). A,B, Colnial stage, C-E, Motile stage, F, Senescent stage.

recently-formed colonies were found on the setae of *Chaetoceros* spp., suggesting this diatom could play a key-role in *Phaeocystis* bloom inception. In the Antarctic other species such as *Corethron* spp., *Chaetoceros* spp., *Fragilariopsis* spp., *Thalassiosira* spp., other particles or sea ice could act as substrate for colony development in the ice-edge zone.

As the bloom evolves, spherical colonies could release from colony-forming diatoms and with melting of sea ice undergo differing development. Part of them keeps spherical form and increase in size, covering a large range of diameter (50 μm - 2 mm). Others change from spherical to elongate form and produce new daughter colonies by budding or division. This differentiation results, at the top of the bloom, in the complex coexistence of a high diversity of colony shapes and sizes.

Phaeocystis antarctica is characterized by a complex

polymorphic life cycle and occurs under at least two different morphological stages as unicellular and colonial (Rousseau *et al.* 1994). In addition, *P. antarctica* may include possible intermediate sexual cycle with coalescing cells producing a rosette of cells that develop into the gelatinous colony (El-Sayed and Fryxell 1993). Fryxell (1989) and Bidigare *et al.* (1996) showed a possible sequence of developing the rosette of cells into the colonial stage. The single unicellular cells are characterized by free-living cells of 3 to 8 μm either flagellated or non-motile. The cells in colonial stage are devoid of flagella, embedded in a muco-polysaccharide matrix. Such colonies range from 10 μm to 9 mm in diameter under natural conditions and their cellular content varies accordingly, from 2 to about 10000 cells (Rousseau *et al.* 1990).

The requirement of a solid substrate has been suggested by several authors as triggering factors for colony formation in natural environment (Boalch 1987; Rousseau *et al.* 1994). From field observations, some diatoms and more particularly some *Chaetoceros* spp. may fulfill the role of substrate. However, recent experimental work under controlled laboratory conditions (Rousseau *et al.* 1994), gives strong evidence that any microscopic particle, either biological (e.g. diatoms), organic or mineral (sand, glasswood, ice) may act as substrate form colony formation. Observational evidence of colony formation mechanisms shows that *Phaeocystis antarctica* in colonial stage is initiated at the early stage of their bloom each by one free-living cell in the sea ice. Although the mechanisms controlling this cellular transformation are still uncertain due to the lack off information on the overwintering *Phaeocystis* forms and on the cell type responsible for colony induction, the existence of haploid microzoospores released from senescent colonies gives some support to sexuality involvement at some stages of colony formation.

Motile stage

In culture observation of *Phaeocystis globosa* (Rousseau *et al.* 1994) free-living cells derived from the transformation of colonial cells consist of five types (Fig. 4). 1) Flagellates or swarmers: These cells were identified as flagellates produced after colony disruption, when initially non-motile colonial cells released from the colonial matrix in the culture medium, develop flagella within a few hours. 2) Non-motile free-living cells: These non-motile free-living cells are similar to colonial cells, in particular with respect to the cell size and cannot be differentiated from colonial cells released into the medium immediately after colony disruption. 3) Microzoospores: Microzoospores are smaller (3-5 μm) than flagellates (3-8 μm) and have been identified in senescent cultures after colony disappearance or in conjunction with non-motile cells and colonies. Microzoospores distinguish themselves from above cell types by their significantly smaller size, and by their half DNA content. Cells have been found in either G1, S or G2 phases of the cell cycle confirming that they are capable of vegetative division. 4) Microzoospores observed by Parke *et al.* (1971): two equal heterodynamic flagella, a short stout haptonema with a distal swelling, an anterior depression, two type of organic body scales, chrysolaminarin vesicles and two chloroplasts. They differ by the presence of superficial vesicles that release a thread-like material forming a five rays star pattern. This feature has been used an important taxonomic criterion to identify different species among *Phaeocystis* free-living cells (see Moestrup 1979). 5) Macrozoospores: These cells were shown to appear inside colonies of 50 to 150 μm in diameter.

Kand & Lee (1995) found that autotrophic nanoflagellates *Cryptomonas* sp. and *Phaeocystis antarctica* in motile stage (Fig. 5C-E) were important carbon contributors in the open waters. The biomass of *P. antarctica* (motile) ranged from 154 to 682 mg C m^{-2} in the upper 100 m, accounting for about 13 % of total PPC. Kang & Lee (1995) suggest that the differences of species composition and biomass are due to regional features of mesoscale hydrography. *Phaeocystis antarctica* in motile stage dominant under certain environmental conditions could be extended to a "marker" that distinguishes water bodies among varying hydrographic regimes.

Senescent stage

Senescent colonies are irregular in shape, less turgid and have a sticky mucus which appears less consistent compared to healthy colonies (Fig. 5F). Senescent colonies are progressively invaded by various auto- and heterotrophic microorganisms and are covered by inorganic detritus, leading to the formation of aggregates of various size and composition at the end of the bloom (Thingstad and Billen 1994). The *Phaeocystis*-derived aggregates composed of mucus, *Phaeocystis* cells, diatoms, ciliates, dinoflagellates and heterotrophic nanoflagellates constitute micro-environments where a complete trophic food-web develops (Weisse *et al.* 1994).

Their sudden disappearance from the water column may result from sedimentation, consumption, disintegration in the water column (Thingstad and Billen 1994; Wassmann 1994; Weisse *et al.* 1994) or advective transportation. Concomitantly with aggregate formation, at the end of the bloom, small flagellate cells similar to the microzoopores described in cultures, were observed to develop inside colonies and subsequently migrate outside.

Factors influencing the fate of senescent *Phaeocystis* blooms are probably water depth, turbulent energy supply, aggregate formation, release of flagellated cells from colonies, microbial degradation, zooplankton grazing as well as lysis of colonies and cells (Wassmann 1994).

Factors regulating the different phases of* Phaeocystis *life cycle

Analysis of the possible environmental factors regulating the transition between the different phases of the life cycle, suggested that 1) nutrient status and 2) requirement of a substrate for attachment of free-living cells would be essential for initiation of the colonial form (Rousseau *et al.* 1994). Physical constraints obviously would be important in determining colony shape and fragmentation although autogenic factors cannot be excluded. Some evidence exists that nutrients regulate colony division, while temperature and nutrient stress would stimulate cell emigration from the colonies.

Rousseau *et al.* (1994) concluded that identification of the over-wintering form and of the first active form preceding colony formation, as well as the mechanisms involved in the transition between free-living cell stage and colony are essential for understanding the occurrence of *Phaeocystis* blooms. A better knowledge of processes of colony division and cell release from colony would allow to estimate the spreading of the colonial stage once initiated. Finally, the relative importance of motility development, of senescent colony and aggregate formation should be further investigated owing to their different ecological role in the bloom termination.

Microbial Degradation of *Phaeocystis antarctica* Material in the Water Column

Observational evidence shows that the large amounts of mucilaginous substances by blooms of *Phaeocystis* colonies largely resist rapid microbial degradation in surface waters of most *Phaeocystis*-dominated ecosystems (Thingstad & Billen 1994). Other factors controlling microbial degradation as the production of antibacterial substances by *Phaeocystis* colonies, cold temperature and lack of inorganic nitrogen and phosphate are further considered. Thingstad and Billen (1994) concluded that nutrient limitation currently observed at the senescent stage of *Phaeocystis* blooms might well explain the low biodegradability of *Phaeocystis* material. However the lack of bacteria attached to colonies during the exponential phase of *Phaeocystis* bloom development are not clearly understood and needs further investigations.

Colonies in early stages of blooms are almost entirely free of attached bacteria (Lancelot and Rousseau 1994; see Fig. 2). Late stationary phase of cultures (Davidson and Marchant 1987) and late bloom stages in natural environments (Billen and Fontigny 1987; Lancelot and Rousseau 1994) are accompanied by increased growth of free living bacteria, along with colonization of the mucus by attached bacteria (Thingstad and Billen 1994). Organic material may accumulate in the water during the senescent phase of blooms (Billen and

Fontigny 1987).

The considerable volume of the colonies, their assumed unpalatability and the limited size of the herbivores (as compared to the size of the colonies) have been suggested to be the cause why *Phaeocystis* colonies are rejected as food by many species of zooplankton (Weisse *et al.* 1994). Likewise, healthy *Phaeocystis* colones keep their surface free for bacteria (Thingstad and Billen 1994) and surface material is not readily mineralized by microbes before the decline of the bloom (van Boekel *et al.* 1992). Grazing on healthy colonies seems, therefore, limited to large meso-zooplankton (e.g. krill). Aggregates and senescent colonies of *Phaeocystis* origin are rapidly colonized by bacteria (Thingstad and Billen 1994), protozoa (Lancelot *et al.* 1991) and diatoms like *Nitzschia* sp. (Estep *et al.* 1990).

The existence of extensive *Phaeocystis* blooms implies that grazing, although influencing the bloom, cannot play an important role during its formation. To the end of the *Phaeocystis* bloom grazing gets more important in deep areas while microbes take care of the rich amounts of suspended organic matter in shallow ones (e.g. Fernández *et al.* 1992). However, the microbial food loop based on *Phaeocystis*-derived matter seems to depend also on DOC which is mainly supplied through lysis of cells (van Boekel *et al.* 1992; Kang *et al.* 1995) and colonies.

As the season progressed, disappearance of *Phaeocystis* colonies in the upper water column corresponded to the appearance of a large bacterial bloom at and below 100 m depth. Putt *et al.* (1994) speculated that in McMurdo Sound, the close alga-bacterial association might enhance remineralization of *Phaeocystis* thus reducing the amount of organic material originating from the bloom which ultimately reaches the sediments.

Sedimentation and Regeneration of *Phaeocystis antarctica* Blooms

Given the significance of *Phaeocystis antarctica* blooms in the Antarctic waters for primary production, factors determining the fate of massive accumulation of suspended biomass during these blooms are important for understanding the ecology of this species as well as the carbon and biogeochemical element cycles of the Antarctic ecosystems. The role of sedimentation plays for the terminaion of *Phaeocystis* blooms which seems to be determined by the physical and biological characteristics of the specific ecosystem where the bloom occurs (Wassmann 1994).

Blooms of *Phaeocystis* colonies and their sedimentation were observed in the Bransfield Strait during ice-free conditions in November/December 1980 (Schnack *et al.* 1985; Von Bodungen *et al.* 1986), the Weddell Sea (Buck and Garrison 1983; Garrison and Buck 1985; Nöthig 1988; Kang and Fryxell 1993; Kang *et al.* 1995) and the Ross Sea (El-Sayed *et al.* 1983; Palmisano *et al.* 1986; SooHoo *et al.* 1987). It is suggested that *Phaeocystis* colonies and diatoms may form aggregates which sink in concert out of the euphotic zone. It is also interesting to note that sediment cores from the area revealed thick mats of *Phaeocystis* on the sediment surface at about 700 m depth, accumulating as sticky mats (Honjo 1990). Based on this preliminary evidence, it appears that (a) the entire water column was traversed within a span of 2 weeks without substantial degradation, that (b) *Phaeocystis* contributed significantly to the food supply of the benthos and that (c) sedimentation indeed seems to be an important factor for the termination of *Phaeocystis* blooms in the ice-edge zones (Fig. 6).

In contradiction to the sedimentation of diatoms, sinking of *Phaeocystis*-derived matter is to a substantial degree disintegrated or mineralized in the upper part of the water column. Sedimentation of phytoplankton-derived matter is governed by the combination of physical and ecological mechanisms. Among the processes, one has to distinguish (a) those speeding up the transport of matter to depth [aggregate formation, sinking and indirectly by herbivory (fecal pellet production)] from (b) those transforming colonies into non-sinking material (cell and colony lysis, disruption of colonies with cell release, hervibory and the subsequent development

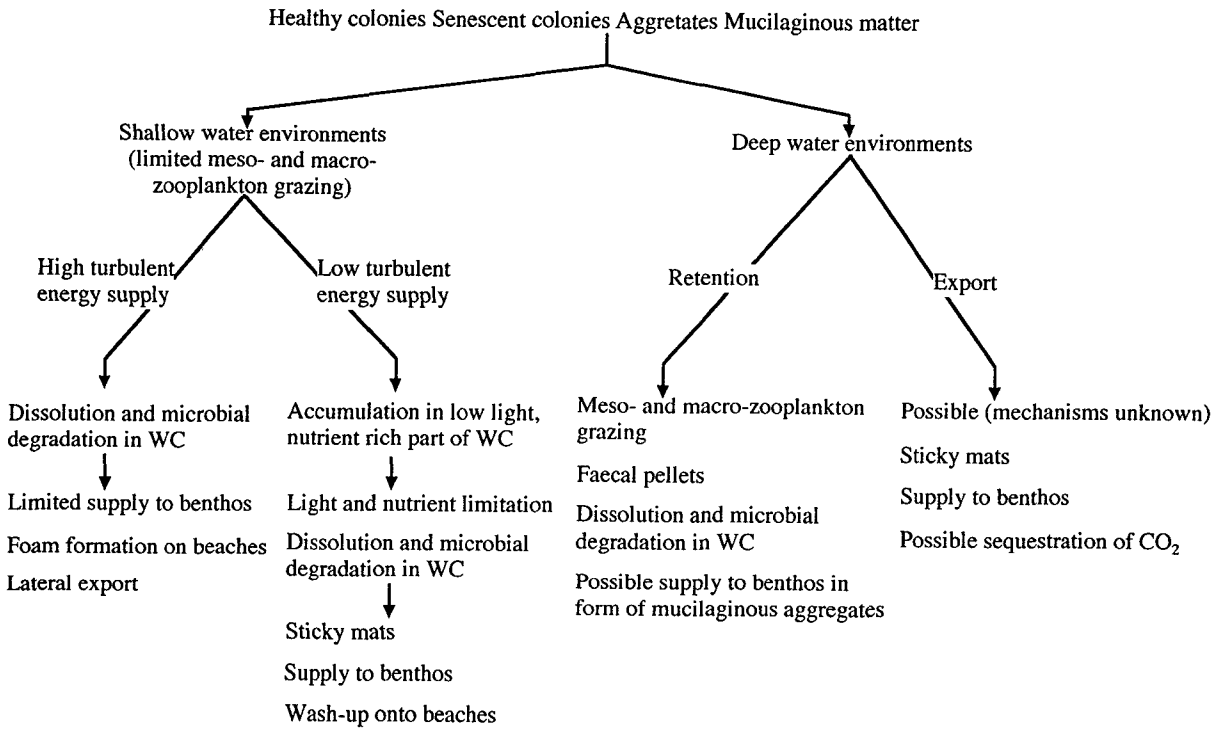

Fig. 6. Hypothetical, simplified scheme on the termination of *Phaecystis* blooms (from Wassmann 1994). WC = water column.

of microbial food webs).

Disappearance of *Phaeocystis*, as for any other phytoplankton bloom, are caused by grazing, autolysis, microbial degradation, and sedimentation (Wassmann 1994). Several points of evidence indicate that *Phaeocystis* appears to be an exemplary organism for the maintenance of nutrient and biomass regeneration of retention food chains controlled by flagellates and the microbial loop: (a) phase alternation between small, single, flagellated cells and large, non-flagellated, gelatinous colonies and vice versa (Rousseau *et al.* 1994), (b) the produciton of extensive amounts of mucus and dissolved organic carbon (DOC) (Lancelot 1983; Billen and Fontigny 1987), (c) the substantial microbial activity on decaying colonies fragments (Thingstad and Billen 1994), (d) reports on positive buoyancy (Skreslett 1988) and (e) the frequent lack of substantial amounts of *Phaeocystis*-derived material in sediment traps exposed at depth.

Ingestion of flagellates, senescent colonies, aggregates and fecal pellets by different size categories of herbivores opens the possibility that particulate and dissolved organic matter derived from *Phaeocystis* blooms is effectively recycled at the end of the bloom and below the euphotic zone (Fig. 6). Given a well structured food-web of planktonic microbes and larger herbivores, good timing as well as sufficient depth, it seems likely that sinking *Phaeocystis* blooms could be mineralized during settling. During such a scenario, *Phaeocystis* blooms strongly support regenerative processes of the planktonic system, resulting in a weak pelagic-benthic coupling (Wassmann 1994).

The formation of aggregates by *Phaeocystis pouchetii* was investigated in coastal water of northern Norway (Passow and Wassmann 1994). Although *Phaeocystis* was observed to form aggregates in some instances, senescent colonies did not have a higher sticking efficiency than growing ones. At senescence *Phaeocystis* colonies appeared to disintegrate. Dissolved carbohydrates derived from the colonial matrix of *Phaeocystis* formed mucous particles which attached to siliceous fibers and glued them together. Detrital mucous flocs formed from a natural particle assemblage and dissolved carbohydrates accumulated during the *Phaeocystis* bloom when rotated. Passow & Wassmann (1994) hypothesized that cells and colonies of *Phaeocystis* may not contribute significantly to vertical flux, but that the

sedimentation of mucous flocs presents a secondary pathway by which carbon assimilated during *Phaeocystis* blooms may sink to greater depth (Fig. 6). While organic-carbon accumulation indicates the significance of disintegration of *Phaeocystis* colonies, post-bloom mucilage sedimentation could be a secondary pathway for the vertical flux of *Phaeocystis*-derived organic matter (Riebesell *et al.* 1995).

The Trophic Significance of *Phaeocystis antarctica* Blooms

Among the processes which may result in disappearance of *Phaeocystis* colonies from the water column are the frequently observed release of flagellated cells from disrupted colonies (Rousseau *et al.* 1994), cell lysis during senescence (van Broekel *et al.* 1992), post bloom dissolution of the mucilaginous matrix in the water column (Veldhuis *et al.* 1986), concomitant accumation of dissolved organic matter in the water column (Eberlein *et al.* 1985) and subsequent microbial degradation (Thingstad and Billen 1994). The growth of bacteria and protozoa depended largely upon dissolved organic carbon (DOC) produced by lysis of *Phaeocystis*. The commonly observed release of flagellated cells from decaying colonies is another mechanism by which *Phaeocystis* can omit sedimentation losses (Rousseau *et al.* 1994). This process gives rise to a separation of living cells and the colony matrix. The flagellated cells can retain in the aphotic or ascent into the euphotic zone. In both cases they are subjected to grazing pressure by protozoa and meso-zooplankton (Weisse *et al.* 1994).

When *Phaeocystis* co-occurs with larger amounts of diatoms, the latter seem to be preferred by some copepod species while others do not select against *Phaeocystis* (Harberman *et al.* 1993). It is unclear whether this is primarily due to unsuitable size of *Phaeocystis* or because it is poor quality food. Protozoa might efficiently control *Phaeocystis* blooms during their initial phases when the share of solitary cells relative to total *Phaeocystis* biomass is higher than during later stages of the bloom. By switching their food preference towards heterotrophic food, copepods might benefit from enhanced protozoan biomass during *Phaeocystis* blooms (Weisse *et al.* 1994).

Schnack (1983) showed that Antarctic copepods with a raptorial feeding mode (*Metridia gerlachi* and *Paruchaeta antarctica*) could feed upon *Phaeocystis*, whereas filter feeding copepods were unable to ingest *Phaeocystis* colonies. Schnack (1983) also found that *Calanus propinquus, Rhincalnus gigas* and *Eucalanus* spp. would not feed on 0.5-1.5 mm colonies of *Phaeocystis*. It was thus relevant to ask if there was some upper limit of colony size which is difficult for copepods to handle and ingest, or if those results of Schnack (1983) and Schnack *et al.* (1985) reflected species-specific feeding behavior. In the Weddell Sea and Bransfield Strait grazing of *Phaeocystis* cells by protozoans (Nöthig and Bodungen 1989) and *Phaeocystis* colonies by krill (Von Bodungen 1986; Smetacek *et al.* 1990; Bathmann *et al.* 1991) are prevailing in the area while grazing by copepods is not likely to be significance (Schnack *et al.* 1985).

Phaeocystis colonies are known for inhibiting diatom populations through release of allelopathic substances (Smayda 1973). Natural phytoplankton contained *Phaeocystis* colonies in association with varying amounts of diatoms (Kang and Fryxell 1993; Kang *et al.* 1995; Bidigare *et al.* 1996). Results from studies on grazing rate of four different copepod species to colonies of *Phaeocystis* in the Barents Sea (Estep *et al.* 1990) indicated that diatoms were actively preyed on in all experiments, with long chain-forming species as the preferred food. Healthy colonies were not consumed, while disintegrating and weakly fluorescent colonies (senescent colonies) were consumed at rates 2-10 times those for chain-forming diatoms.

Previous studies suggest that growth and reproduction of antarctic krill (*Euphausia superba*) are generally food limited in the southern oceans. Although antarctic krill are primarily herbivores, it is not known whether they ingest and assimilate different types of phytoplankton with similar rates and efficiencies. Such knowledge is important if we want to

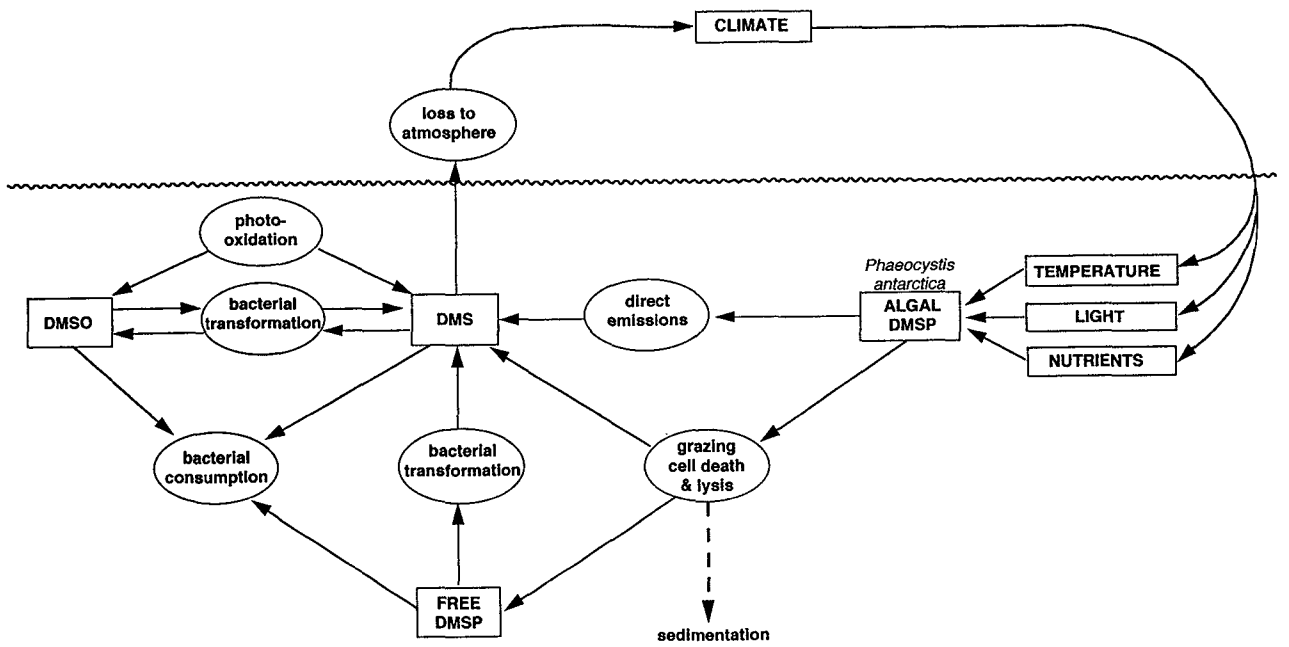

Fig. 7. The marine biogeochemical cycle of dimethyl sulphide (DMS); production, transformation and utilisation pathways which may ultimately influence the amount of DMS lost to the atmosphere (from Liss *et al.* 1994).

understand how the patterns of phytoplankton abundance and species composition affect the krill's food availability (Haberman *et al.* 1993). In particular, can food availability be accurately determined from measurements of total chlorophyll, or do we need to use more detailed measurements of species composition? Haberman *et al.* (1993) reported the results of preliminary experiments comparing the ingestion rates of krill on diatoms to those on *Phaeocystis* sp. in laboratory feeding experiments.

Dimethyl Sulfide (DMS) and *Phaeocystis antarctica*

Dimethyl sulfide (DMS) is the dominant sulfur gas found in surface marine waters and there is compelling evidence that it is formed biologically in these environments (Liss *et al.* 1994). In all areas so far investigated the oceans are found to be highly supersaturated (typically by two orders of magnitude) with respect to atmospheric levels of DMS, which indicates a net flux of the gas out of the oceans (Fig. 7). The importance of marine biogenic DMS produced by *Phaeocystis* is with respect to aspects of environmental chemistry, i.e. the global sulphur cycle, acidity of rain and aerosols and in the formation of cloud condensation nuclei with their implications for the radiation budget of the Earth.

Phaeocystis bloom link the oceanic and atmospheric compartments of the carbon and sulfur cycles. A large portion of carbon incorporated by the colonial stage of *Phaeocystis* is released extracellularly, in particular in stationary colonies. In *Phaeocystis* cellular and extracellular carbon incorporation represent different uptake rates. Matrai *et al.* (1995) observed little extracellular carbon production by cells at high irradiance, and maximal rates were observed at intermediate irradiance. Newly incorporated carbon that accumulates in the mucilage of the colonial stage of *P. antarctica* during photosynthesis was not reutilized for cellular growth during the dark period, as observed for temperate clones. The production of DMS was an order of magnitude higher for *Phaeocystis* than for diatoms. Stationary colonies had higher DMS and dissolved DMSP production rates than exponentially growing ones.

Dimethyl sulfide (DMS) emissions by marine phytoplankton may have significant effects on both local and global climate due to the formation of cloud condensation nuclei and possible feedback loops between phytoplankton production and cloud

albedo effects (Malin *et al.* 1992). Satellite images from the Coastal Zone Color Scanner (CZCS) have revealed the regular occurrence of phytoplankton spring blooms near the Antarctic Peninsula (Cominso and Sullivan 1986). These spring blooms are frequently composed of the colony-forming *P. antarctica* (Fryxell and Kendrick 1988; Kang and Fryxell 1993; Bidigare *et al.* 1996). This prymnesiophyte contains very high concentrations of the DMS precursor, dimethylsulfoniopropionate (DMSP) per unit biomass compared to other species of marine phytoplankton (DiTullio and Smith 1996). As a consequence, DMS emissions during a *Phaeocystis* bloom may be substantial. The primary source of DMS is dimethylsulfoniopropionate (DMSP) in phytoplankton, but the mechanisms governing DMSP decomposition to DMS remain uncertain. DMS concentrations in the ocean vary spatially and temporally depending on phytoplankton species and abundance; in particular, dinoflagellates and prymnesiophytes (for example, *P. antarctica*) produce significant amounts of DMS during cell senescence (DiTullio and Smith 1996).

Dimethylsulfide (DMS) concentrations in sea water were found to be high (0.19 to 390 nM) in an Antarctic bloom of *Phaeocystis antarctica* during October and November 1990 (Crocker *et al.* 1995). DMS concentrations were positively correlated with algal pigments, particularly 19'-hexanoyloxyfucoxanthin, a prymnesiophyte pigment. Since oceanic DMS production has been linked to the global albedo through the formation of cloud condensation nuclei, light-mediated changes in DMS concentrations may affect the global climate.

Baumann *et al.* (1994b) observed that mucoid species, *Phaeocystis antarctica* in colonial stage and *Chaetoceros socialis*, produced more DMS than the other diatoms. DMS release was higher at low light and low temperature. Full light (UV-B + UV-A + PAR) caused the strongest decrease in the production of DMSP contents produced by *P. antarctica* (Hefu and Kirst 1997). Hefu and Kirst (1997) hypothesized that DMSP production in *P. antarctica* was inhibited by UV radiation. The effect of UV radiation on DMSP production and oxidation of DMS may be an important factor in the variability of DMSP and the global flux of DMS from ocean to atmosphere.

Response of *Phaeocystis antarctica* to UV-B Fluctuations

Phaeocystis antarctica is widely distributed in Antarctic waters, and forms massive near-surface blooms in the marginal ice-edge zone. UV irradiance in the Antarctic marine environment is reportedly as high in Oct and Nov as in mid-summer due to stratospheric ozone depletion. Because of the location and timing of the *P. antarctica* bloom, this prymnesiophyte has been exposed to high levels of UV-B (280 to 320 nm) radiation. Colourless water-soluble compounds, produced by the colonial stage in the life cycle of this alga, absorb strongly between 250 and 370 nm, with absorbance maxima at 271 and 323 nm and may provide UV protection to this alga (Marchant *et al.* 1991a, b).

Numerous studies have documented the initiation, development and decline of *Phaeocystis* blooms (Rousseau *et al.* 1994; Wassmann 1994). Decline in cell number in Antarctic waters has been attributed to two major factors: sedimentation of cells (Wassmann *et al.* 1990; Smith 1993) and cell lysis (Verity *et al.* 1988; Fernández *et al.* 1992; van Boekel *et al.* 1992). The most probable cause of the cell loss observed under ozone depletion is cell lysis resulting from cell death mediated by increased exposure to UV-B (Karentz and Spero 1995).

Karentz & Spero (1995) observed that *Phaeocystis* populations responded negatively to increased UV-B (Fig. 8). It is of interest to note that this did not give co-occurring diatom species a competitive edge as Bidigare *et al.* (1996) observed (Fig. 9). The increased ratio of diatoms to *Phaeocystis* cells was closely correlated to the temporal gradient and showed a lower correlation to changes in ozone (Bidigare *et al.* 1996). The reduction in cell densities of *P. antarctica* observed with decreasing ozone suggests death of cells owing to increased UV-B exposure. Subsequent increases in cell numbers occurred

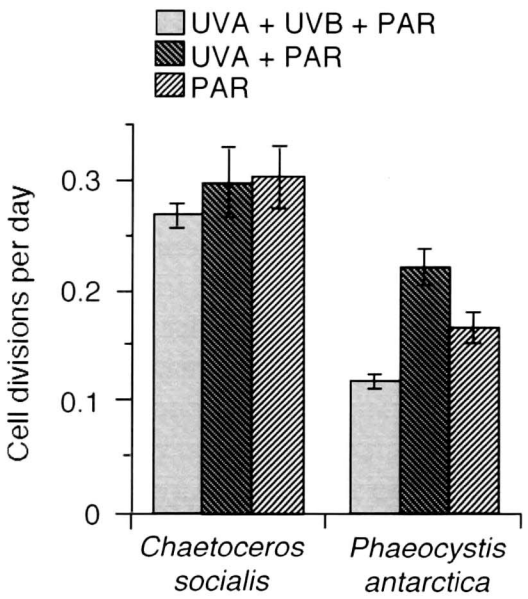

Fig. 8. Cell division rates for *Chaetoceros socialis* and *Phaeocystis antarctica* under partioned solar light regimes as described in Figure 5 of Bidigare *et al.* (1996).

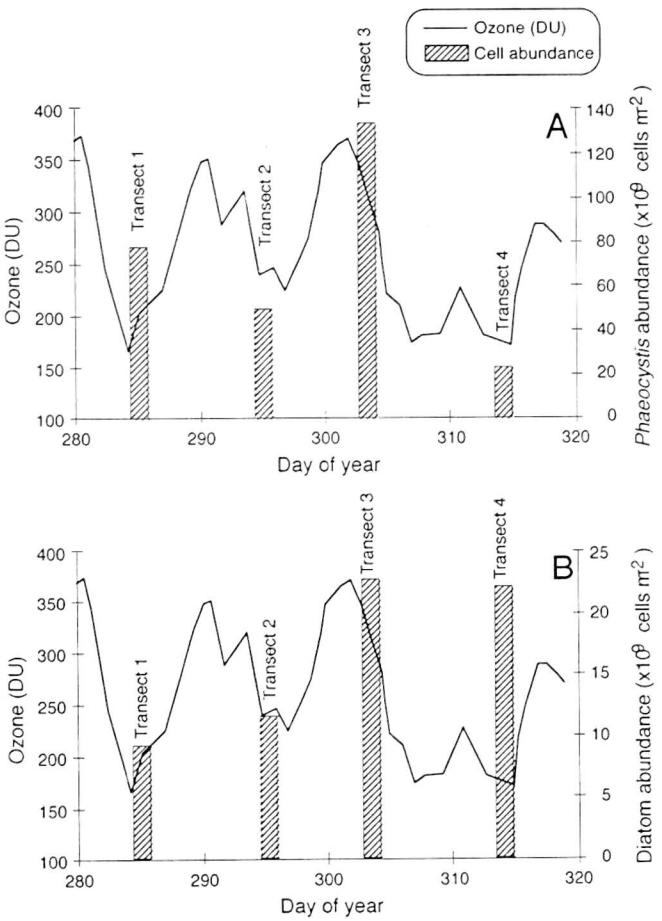

Fig. 9. Ozone concentration (Dobson Unit, DU) versus integrated abundace of *Phaeocystis antarctica* and diatoms in the upper 115 m near marginal ice-edge zone of Bellingshause Sea during the Icecolors' 90 expedition (from Bidigare *et al.* 1996).

during increasing of ozone.

The overall physiological impact of increased UV-B exposure on *Phaeocystis antarctica* would presumably shift the balance between photosynthesis and respiration. Not only are the structural and physiological components of the photosynthetic pathway directly affected by UV-B (Karentz 1994), but it is assumed that a greater proportion of photosynthate will be respired to provide energy for various repair and recovery mechanisms employed by cells. Karentz & Spero (1995) used ratio of carbon isotopes to see changes in the overall photosynthetic or respiratory physiology of *Phaeocystis* cells and observed that this species was very sensitive to elevated UV-B levels.

As discussed in Kang & Fryxell (1993), *Phaeocystis antarctica* seems to have a selective advantage over other phytoplankton in light-controlled or light-limited environments. Palmisano *et al.* (1986) found that *P. antarctica* showed a 3- to 4-fold increase in photosynthetic efficiency per chlorophyll *a* and a 2- to 3-fold increase in photosynthetic efficiency per cell in a reduced growth irradiance beneath annual sea ice. The photoadaptive strategies of *P. antarctica* that is capable of physiologically adapting to low irradiances seem feasible, because protein synthesis by the colonial *P. antarctica* continues at the expense of the extra-cellular muco-polysaccharides synthesized under the light limitation (Lancelot and Mathot 1985).

Although the ecological impact of ozone depletion is not well understood, the biologically detrimental effects of UV-B exposure on phytoplankton are well documented (Karentz 1994). It is reasonable to assume that increasing UV-B exposure increases the physiological stress on microalgal cells in the Antarctic, causing decreases in photosynthetic efficiency and cell survival. Although Antarctic *Phaeocystis* contain UV-absorbing compounds such as MMAs, studies conducted under artificial and ambient light indicate that *Phaeocystis* appears to have greater sensitivity to UV-B exposure than Antarctic diatom species (Marchant *et al.* 1991a, b;

Smith *et al.* 1992; Davidson and Marchant 1994a, b; Karentz 1994; Karentz and Spero 1995; Bidigare *et al.* 1996).

Duration of O_3-dependent UV-B exposure seems to be another important factor influencing *Phaeocystis antarctica*. This hypothesis seems feasible, because *P. antarctica* abundance was closely related with the ozone concentration when the temporal variation of ozone concentrations during a 6-week cruise (Icecolors '90) in the marginal ice zone of the Bellingshausen Sea (Karentz and Spero 1995; Bidigare *et al.* 1996) were compared with mean integrated absolute abundance of *P. antarctica*. Dramatic change of *P. antarctica* abundance was observed, while the diatom cells showed no dramatic change in cell numbers (Fig. 9). The mean abundance of *Phaeocystis antarctica* in transect 3 where Smith *et al.* (1992) found the highest ozone concentration (~350 DU) during staying in the study area were about 2-6 times higher than those in transects 1, 2 and 4 where they observed increases in UV-B radiation due to ozone depletion (~170-220 DU).

Phaeocystis antarctica was more sensitive in UV-B radiation than diatoms. During Icecolors '90 cruise, Karents & Spero (1995) attempted to elucidate UV-specific effects on Antarctic phytoplankton by measuring growth rates of unialgal cultures of centric diatom *Chaetoceros socialis* and *P. antarctica*. The results of the study (Fig. 8) showed that UV-B inhibition of growth rate was much greater for a *P. antarctica* than for a clone of the diatom *Ch. socialis*, indicating the higher vulnerability of *Phaeocystis* to decreasing stratographic O_3 level than that of diatoms. In contrast to diatoms, the concentrations of pigments with discrete UV absorption peaks in *P. antarctica* were high and changed significantly under increasing UV-B irradiance (Davidson *et al.* 1994a, b). Survival of *P. antarctica* under elevated UV-B irradiances results from processes of screening mechanisms (MMAs).

Numerous investigators have demonstrated marked interspecific differences in tolerance of Antarctic marine phytoplankton to UV-B exposure (Karentz *et al.* 1994; Davidson and Marchant 1994a,b; Bidigare *et al.* 1996). Consequent changes in species composition have been proposed but as yet not demonstrated. Davidson & Marchant (1994a) demonstrated UV-B-induced changes in species composition favouring the colonial stage of *Phaeocystis antarctica*, and their data indicate the potential for altered trophodynamics and carbon flux in Antarctic waters as a result of ozone depletion.

Rotation of the Antarctic polar vortex resulted in change in ozone concentrations (170-380 Dobson units) over regions of the marginal ice zone of the Bellingshausen Sea (Smith *et al.* 1992). The changes in ozone caused significant variations in incident and in-water UV-B fluences. *Phaeocystis antarctica* was the dominant phytoplankton taxon and cell numbers were positively correlated to ozone. The densities of co-occurring diatoms were not related to changes in ozone. These observations suggest that *Phaeocystis antarctica* responds very rapidly and adversely to increased UV-B exposure and may be a useful indicator species for assessing the any changes of Antarctic marine communities relative to increased UV-B levels (Karentz and Spero 1995; Bidigare *et al.* 1996).

Future Questions to be Addressed

The observed long-term increase of *Phaeocystis* bloom occurrences in the Antarctic waters gives support of the good adaptability of colony forms to growth in the changing environment (Kang and Fryxell 1993; Davidson and Marchant 1994a; Bidigare *et al.* 1996), rendering *Phaeocystis* appears to be useful as indicator species of long-term and/or chronic environmental changes, such as climate and environmental changes (e.g. eutrophication, UV-B effects, global warming).

Questions to be addressed in the future are 1) factors controlling inception and regulation of *Phaeocystis antarctica* blooms; 2) physiology, taxonomy, and life cycle of *P. antarctica*; 3) factors controlling development of colonial forms and free-living forms; 4) trophic significance of *Phaeocystis* blooms (i.e. overall functioning of *Phaeocystis*-dominated

ecosystems and their global significance); 5) DMS production and emission into the atmosphere; 6) grazing of the different *Phaeocystis* morphotypes by protozoa and meso/metazooplankton; 7) microbial decomposition of *Phaeocystis* colonies; 8) formation of aggregates; 9) sedimentation of *Phaeocystis* material; 10) what extent these grazing and sedimentation processes operate on an ecosystem scale, i.e. when and where *Phaeocystis* does function as a link or a sink to higher trophic levels; 11) role of UV-B protecting (absorbing) components, colorless water-soluble components of *Phaeocystis* colonies which consist of cells embedded in the mucilaginous matrix.

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