

Factors controlling the distribution of diatoms and *Phaeocystis* in the Ross Sea

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Abstract

The spatial and temporal distributions of phytoplankton pigments were investigated in the western and south central Ross Sea during austral spring 1994 and summer 1990. Large gradients in biomass and phytoplankton community composition were observed both in the east–west and south–north directions, in relation to differences in water column structure and stability, which themselves depend on the processes of ice retreat within the different areas. Important are melting in the western Ross Sea, which induces strong stratification, and ice breakup and wind stress in the south central Ross Sea, which result in deep mixing and weakly stratified waters. In the western Ross Sea, the highest chlorophyll *a* (chl. *a*) concentrations observed in this study (129–358 mg m⁻² in the upper 100 m) were tightly coupled to the stratified region of meltwater influence and were dominated by diatoms, as indicated by elevated fucoxanthin concentrations (89–239 mg m⁻² in the upper 100 m). In the diatom bloom area, high levels of phaeophorbides *a* (maximum value of 192 mg m⁻² in the upper 100 m) indicated that the dominant grazers, identified as *Limacina helecina* and copepods [Hecq, J.H., Magazzù, G., Goffart, A., Catalano, G., Vanucci, S., Guglielmo, L., 1992. Distribution of planktonic components related to vertical structure of water masses in the Ross Sea and the Pacific sector of the Southern Ocean. In: Anonymous, Atti del 9° congresso A.I.O.L., Santa Margherita Ligure, 20–23 Novembre 1990, 665–678], transferred a sustained part of the diatom production to the herbivore trophic level. Synthesis of our data with published information suggests that the diatom bloom we observed in the western Ross Sea was dominated by the species *Fragilariopsis curta*, and occurs annually off the coast of Victoria Land from 72°30'S to 77°S within 100–250 km from the coastal ice edge. It is assumed to persist on the order of 2.5–3 months during summer. In the south central Ross Sea, which was characterized by a poorly or unstratified water column, moderate chl. *a* concentrations (55–186 mg m⁻² in the upper 100 m) were found in the polynya and in the ice-edge area in early spring. The 19'-hexanoyloxyfucoxanthin (19'-HF), a biomarker for *Phaeocystis*, was the major contributor to the total carotenoid abundance (29–132 mg m⁻² in the upper 100 m), corroborating the hypothesis that *Phaeocystis* are well adapted to develop in a relatively mixed water column. At the northern limit of the polynya, a quite narrow (ca. 30 km) diatom bloom (31–67

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mg fucoxanthin m^{-2} in the upper 100 m) overlapped with the *Phaeocystis* bloom in the slightly stratified marginal ice zone. This was an area of increased grazing pressure by various types of herbivorous zooplankton, among which very large amounts of krill were observed. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

At the beginning of the austral summer, the usual season of oceanographic cruises in the Southern Ocean, the coastal regions, the ice edges and the frontal zones are often the site of remarkable phytoplankton blooms, both in the ice and in open water. In these areas, massive diatoms blooms are frequently observed (e.g. El-Sayed, 1970; Heywood and Priddle, 1987; Fryxell and Kendrick, 1988; Knox, 1994). These observations support the classical concept of the Antarctic marine food chain (diatoms–krill–whales), giving large diatoms a predominant position in the pelagic system (Guillard and Kilham, 1977). However, during the last two decades, it has been recognized that algal taxa belonging to the “less than 10 μm ” community may predominate under certain conditions (Jacques and Panouse, 1991; Jochem et al., 1995). Attention has been paid to the role of the small diatoms (3–6 μm in length), which often constitute the bulk of the phytoplankton community (Knox, 1994), and to the presence of prymnesiophytes and other flagellates, which may contribute significantly to the total phytoplankton biomass (Gieskes and Elbrächter, 1986; Andreoli et al., 1995; Barlow et al., 1998).

Satellite imagery has revealed that among the greatest accumulations of phytoplankton around the Antarctic continent occur in the Ross Sea, where large coastal polynyas develop during the spring (Comiso et al., 1993; Arrigo and McClain, 1994). Although surface waters in the Ross Sea generally have sufficient nutrients to sustain phytoplankton growth (Nelson and Tréguer, 1992; Tréguer et al., 1994), a high degree of spatial biological variability and substantial gradients in phytoplankton biomass, primary production and nutrients fields are observed between the western and the south central regions (e.g. El-Sayed et al., 1983; Gordon, 1994; DiTullio and Smith, 1996; Catalano et al., 1997).

In the western Ross Sea, maps of pigment concentration determined by analysis of CZCS imagery

revealed that an intense phytoplankton bloom developed by mid-December in the Terra Nova Bay polynya (Arrigo and McClain, 1994). Later in the season (January–February), field studies conducted between 72°30'S and 77°S revealed that extensive diatom blooms are produced by the receding ice edge off the coast of Victoria Land. Such blooms occur annually, and extend 100–250 km out from the dense pack-ice (Smith and Nelson, 1985; Wilson et al., 1986; Nelson and Tréguer, 1992; DiTullio and Smith, 1995; Nelson et al., 1995). The high-biomass core of phytoplankton is confined to a lens of low-salinity meltwater which coincides spatially with the region of greatest nutrient depletion (Smith and Nelson, 1985; Nelson and Smith, 1986), indicating a long and intense period of production. The dominant species in the bloom is the nanoplanktonic pennate diatom *Fragilariopsis curta*, which constitutes up to 85% of the total cell number (Smith and Nelson, 1986).

In the south central Ross Sea, which includes the region where the first open water appears in spring with the formation of the Ross Sea polynya (Arrigo et al., 1998; Hecq et al., 1999), *Phaeocystis* spp. blooms are observed in the weakly stratified waters. *Phaeocystis* blooms typically develop from November to February (El-Sayed et al., 1983; Palmisano et al., 1986; Smith and Gordon, 1997) and appear to be localized approximately south of 76°S, between the Ross Ice Shelf and the 500 m depth shelf break (Ainley and Jacobs, 1981; El-Sayed et al., 1983). In McMurdo Sound, blooms of *Phaeocystis* are a regular annual event (Knox, 1990). Smith and Gordon (1997) suggest that the onset of the phytoplankton growth in the southern Ross Sea occurs at the beginning of October, which is substantially earlier than has been observed in the water column anywhere in the coastal Antarctic, and emphasizes the hyperproductive nature of the Ross Sea polynya.

Several related factors have been proposed to explain the variability of phytoplankton development within the Ross Sea, such as meteorological condi-

tions (Arrigo et al., 1998), sea ice extent, type and thickness (Leventer and Dunbar, 1996), stratification of the water column (Smith and Nelson, 1985), light levels in the photic zone (El-Sayed et al., 1983), and iron concentrations (Martin et al., 1990; Sedwick and DiTullio, 1997). However, the causes and the magnitude of the spatial and temporal variations in phytoplankton communities in the western and south central Ross Sea are not completely understood. Moreover, the fate of the phytoplankton blooms is still largely unknown, although the large zooplankton and marine mammals' populations depend ultimately on primary producers at the base of the food web.

The first objective of this paper is to examine the spatial and temporal distributions of phytoplankton in the western and south central Ross Sea, during the austral spring (November–December) and summer (January), using pigments measured by HPLC as

biomarkers. The pigment data are related to nutrient conditions and physical structure of the water column in order to provide insight into the factors controlling the composition of the phytoplankton community. The second objective is to discuss the role that the processes of ice melting, polynya opening, and zooplankton grazing might have on phytoplankton dynamics in the western and south central Ross Sea.

2. Material and methods

Field studies took place as part of the Italian National Antarctic Program and were conducted in the Ross Sea during cruises in two separate years (Fig. 1, Table 1). The first set of data was collected during the austral summer (5th Italian Antarctic Expedi-

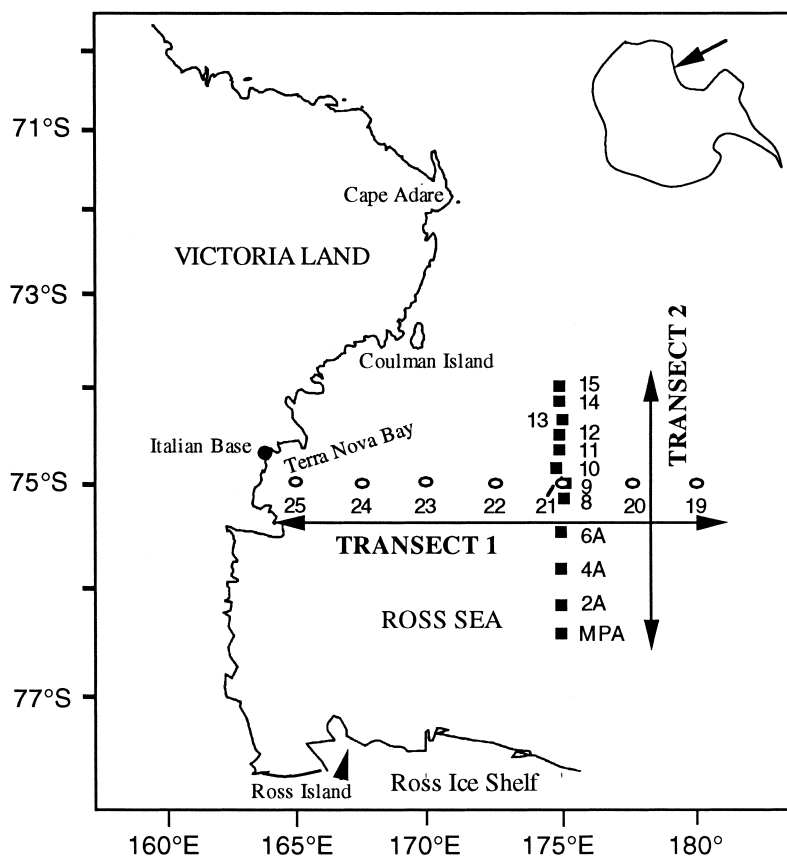


Fig. 1. Map of stations location during this study.

Table 1

Position and calendar of the transects used in this study

Transects	Stations	Latitude	Longitude	Period
Transect 1	19, 20, 21, 22, 23, 24, 25	75°S	165°02'E–179°56'E	01–06 January 1990
Transect 2	MPA, 2A, 4A, 6A, 8, 9, 10, 11, 12, 13, 14, 15	76°27'S–73°59'S	175°E	20–26 November 1994

tion), along an east to west transect at 75°S, from the open water to the Terra Nova Bay polynya (transect 1). On the “Rossmize” cruise, a south–north section across the Ross Sea polynya was sampled in November at 175°E, following the northward ice retreat (transect 2). The Rossmize cruise represents one of the earliest entries into the Ross Sea polynya during the austral spring by an oceanographic vessel.

Along transect 1, vertical sampling was carried out on hydrographic stations by means of twelve 10-l Niskin bottles attached to a CTD rosette. Samples from transect 2 were collected with a SBE 32 Carousel sampler, equipped with twenty-four 12-l Niskin bottles. In the upper 200 m, standard sampling depths were the surface, 10, 25, 50, 100 and 200 m. Moreover, 2–5 variable depths were added to the hydrological casts according to the stratification and the attenuation of incident PAR.

Continuous depth profiles of temperature and salinity were collected at each station. Density values were computed from these data and are reported in Artegiani et al. (1992) and Russo et al. (1997). Because water-column stability is an important controlling factor for the biomass and structure of phytoplankton communities, E_{\max} ($\text{m}^{-1} \times 1000$), the stability index of the depth corresponding to the maximum density gradient, was calculated according Mitchell and Holm-Hansen (1991) and Catalano et al. (1997).

During the 5th Italianartide Expedition, nitrate and silicate concentrations were determined on board by means of a Technicon II Autoanalyser (Hansen and Grasshoff, 1983) while during the Rossmize cruise, an Alpkem autoanalyser was adopted according to ALPKEM (1992a,b).

Samples of 1 l for pigment determination were filtered at low vacuum pressure through Whatman GF/F filters. They were immediately frozen at –25°C until analysis on board, some hours later. Frozen filters were extracted in 100% methanol us-

ing grinding and refiltration to remove cellular debris. Phytoplankton pigments and their degradation products were separated and quantified by high performance liquid chromatography (HPLC), following the procedures of Mantoura and Llewellyn (1983) and Williams and Claustre (1991), for the 5th Italianartide and Rossmize cruises, respectively. Chlorophyll *a* (chl. *a*) is used as the universal index of phytoplankton biomass. Fucoxanthin and 19'-hexanoyloxyfucoxanthin (19'-HF) are used as chemotaxonomic tools to identify diatoms (Jeffrey, 1980; Claustre et al., 1994; Barlow et al., 1998) and prymnesiophytes, respectively (Gieskes and Kraay, 1986; DiTullio and Smith, 1995; Jeffrey et al., 1997). Prymnesiophytes are very common in the Ross Sea and consist mainly of *Phaeocystis antarctica* (Innamorati et al., 1990; Marino and Cabrini, 1997). Among the phaeopigments, phaeophorbides *a* are here considered. They are produced from the breakdown of chl. *a* by the enzymatic activity of the zooplankton digestive system, and are utilized here as a quasi-conservative tag for the detection of ingestion of phytoplankton by feeding herbivores (Jeffrey, 1974; Welschmeyer and Lorenzen, 1985; Vernet and Lorenzen, 1987; Jeffrey et al., 1997).

3. Results

3.1. Western Ross Sea: transect 1

On the first cruise, transect 1 was situated in a region of open water with drifting ice floes. The pack-ice edge was located between the coast of Victoria Land and the westernmost station (station 25). The major feature of the hydrographic field was a well-established lens of low-density low-salinity surface water from station 22 to station 25 (Fig. 2). Within this stable surface layer, almost certainly produced by ice melt, a very strong thermohaline

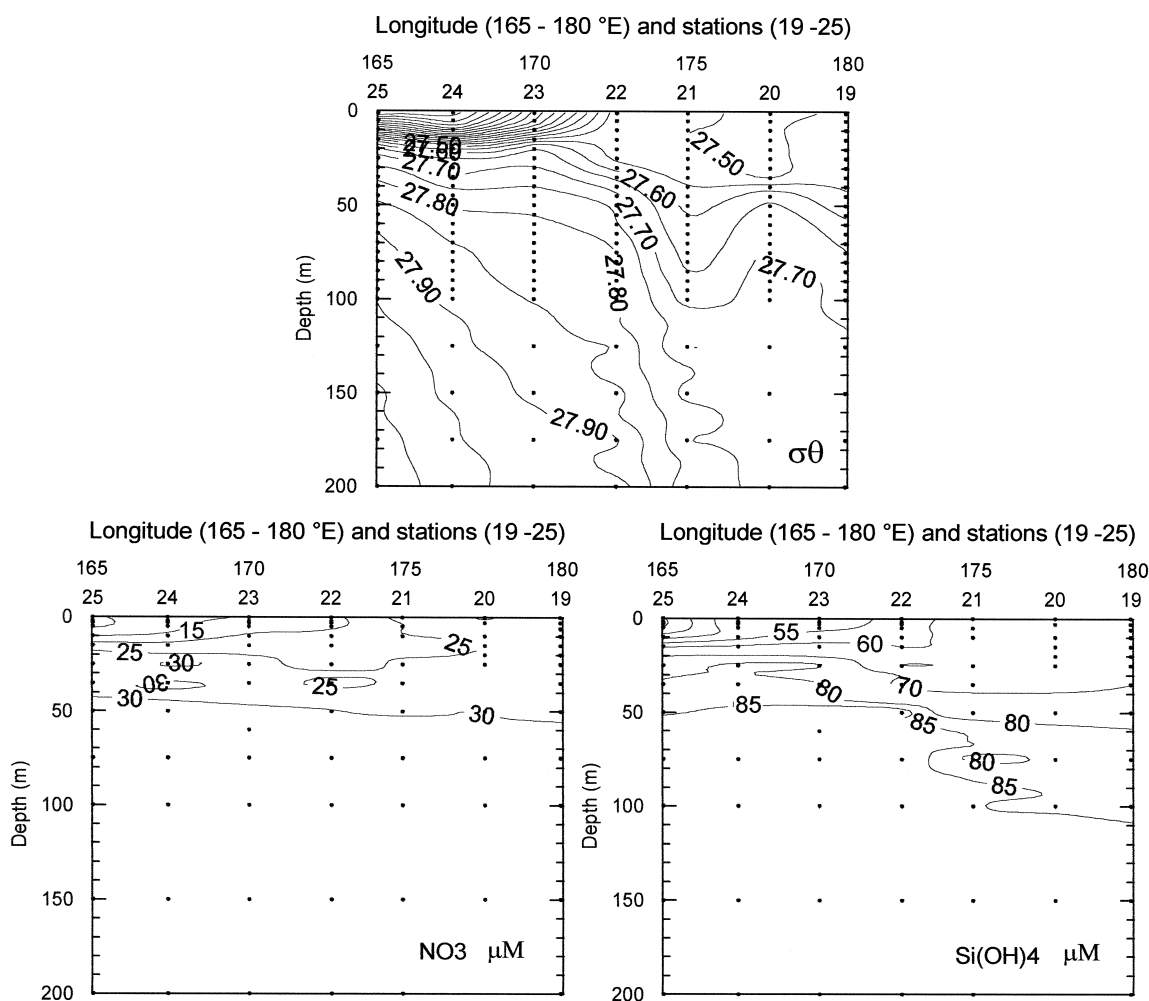


Fig. 2. Distribution of σ_θ , nitrate (μM) and silicate (μM) in the upper 200 m along transect 1. σ_θ data from Artegiani et al. (1992).

gradient was observed, with temperature and salinity varying from values $> 1^\circ\text{C}$ and < 33.4 at the surface to values $< -1.6^\circ\text{C}$ and > 34.5 at 30 m (data from Artegiani et al., 1992). As a whole, a stable upper mixed layer prevailed for the westernmost stations (stations 22–25), with E_{max} varying from 21 to $107 \text{ m}^{-1} \times 1000$. Lower values of E_{max} in eastern part of the section ($7\text{--}22 \text{ m}^{-1} \times 1000$) indicated a less stable water column.

Fig. 3 shows the spatial variation of chl. *a*, fucoxanthin, 19'-HF and phaeophorbides *a* along transect 1. Horizontal distribution of values integrated through the upper 100 m is also presented. As regards inte-

grated chl. *a* concentrations, a west–east gradient was observed, with a core of biomass over $125 \text{ mg chl. } a \text{ m}^{-2}$ in the upper 100 m extending seaward for approximately 220 km (stations 25–22). Maximum integrated chl. *a* reached $358 \text{ mg chl. } a \text{ m}^{-2}$ at station 22 and was then followed by a drastic decrease of concentrations proceeding eastward. An area of moderate chl. *a* concentrations was situated at the eastern end of the transect, around station 20.

Fucoxanthin was the most abundant carotenoid on this transect, and its distribution was similar to that of chl. *a* (Fig. 3). Diatom biomass, as estimated from fucoxanthin concentrations, was greatest in the upper

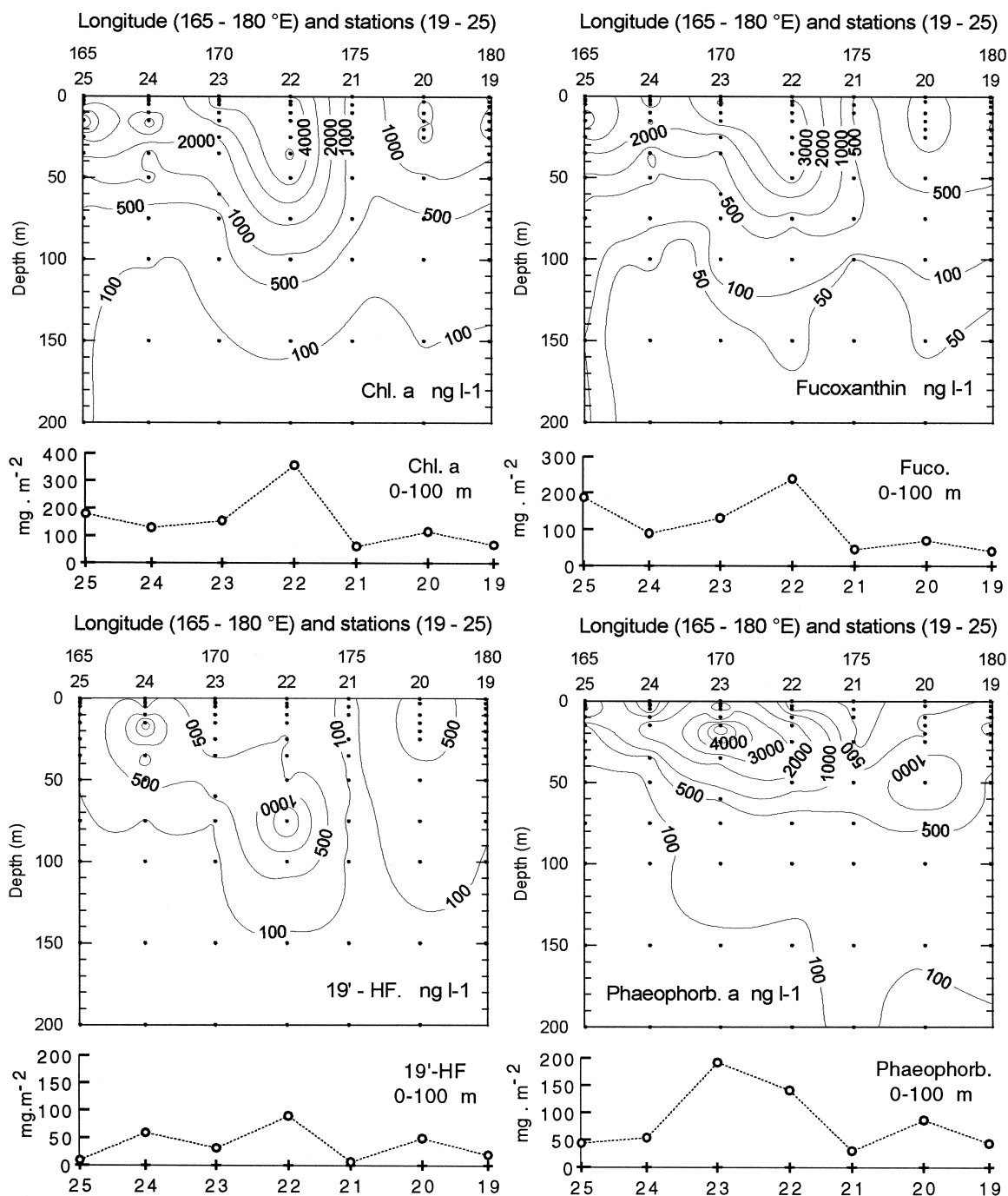


Fig. 3. Distribution of chl. *a*, fucoxanthin, 19'-HF and phaeophorbides *a* in the upper 200 m along transect 1 (ng l⁻¹). Integrated biomasses (0–100 m, mg m⁻²) are shown below each section.

50 m of the western portion of the transect and decreased markedly east of station 22. In the western

part of the section, integrated fucoxanthin concentrations in the upper 100 m ranged from 89 to 239 mg

m^{-2} , and reached a maximum value at station 22, where chl. *a* concentration was maximum.

Integrated 19'-HF, the second most dominant chromophytic pigment, did not show any clear trend of variation moving along the transect. However, the vertical distribution of 19'-HF exhibited a contrast between the western and the eastern parts of the section. In the western part, maxima of 19'-HF concentrations were generally observed below those of fucoxanthin whereas maxima of 19'-HF and fucoxanthin concentrations coincided in the area of moderate chl. *a* concentrations around station 20 (Fig. 3). Moreover, while fucoxanthin concentration de-

creased rapidly with depth, the vertical gradient in 19'-HF concentration was less pronounced.

High levels of phaeophorbides *a* were found at the stations where chl. *a* concentrations were elevated (Fig. 3). In the western part of the section, the vertical distribution of phaeophorbides *a* followed the patterns of chl. *a* and fucoxanthin. The maximum integrated concentration of phaeophorbides *a* was seen in the central part of the diatom bloom, and reached the exceptionally high level of 192 mg m^{-2} in the upper 100 m at station 23.

The high-biomass region of the bloom was an area of pronounced silicate and nitrate depletions

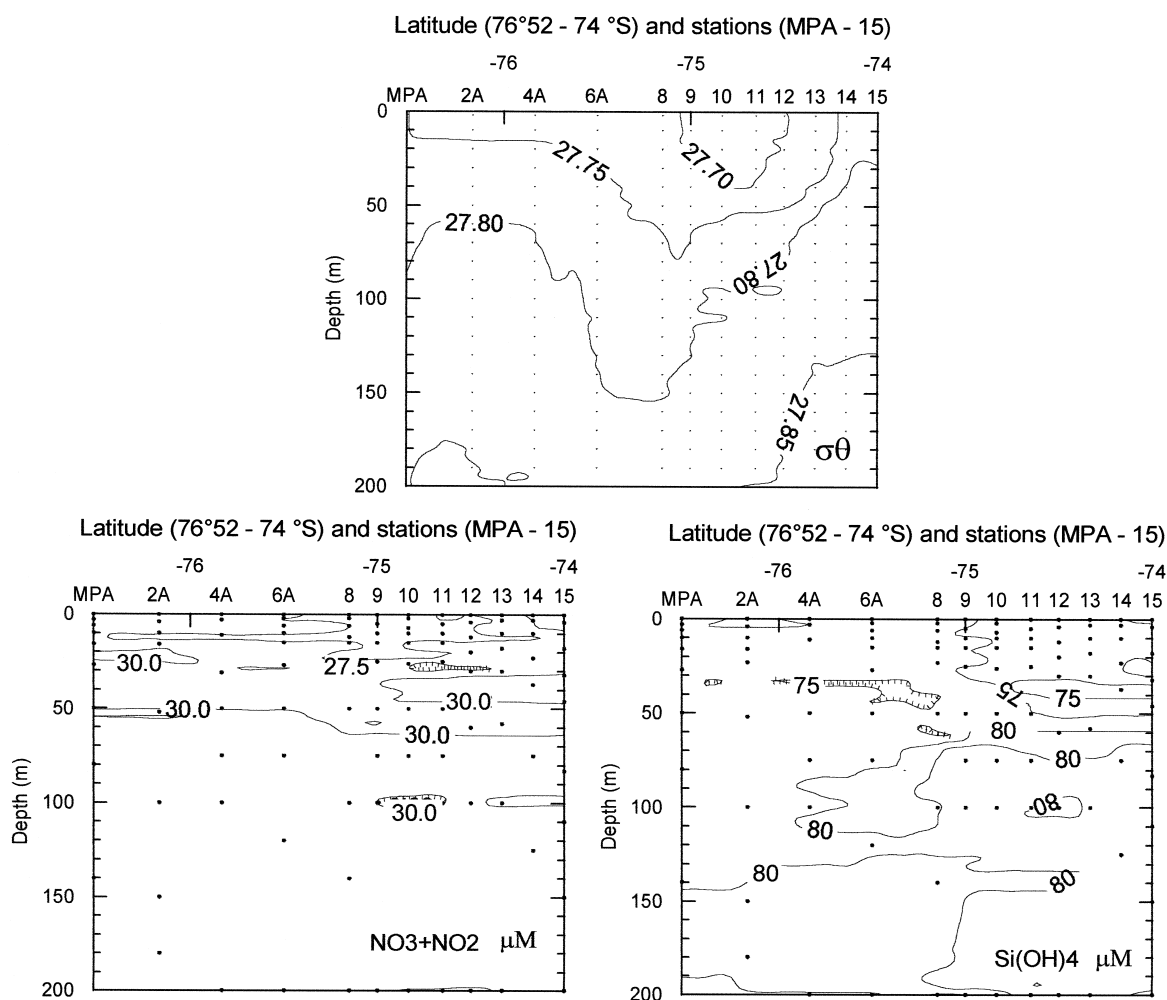


Fig. 4. Distribution of σ_θ , nitrate + nitrite (μM) and silicate (μM) in the upper 200 m along transect 2. σ_θ data from Russo et al. (1997).

(Fig. 2) with their concentrations reduced by up to 30% of the winter values (deduced from the values

taken immediately below the pycnocline). The most intense nutrient removal occurred for silicate, which

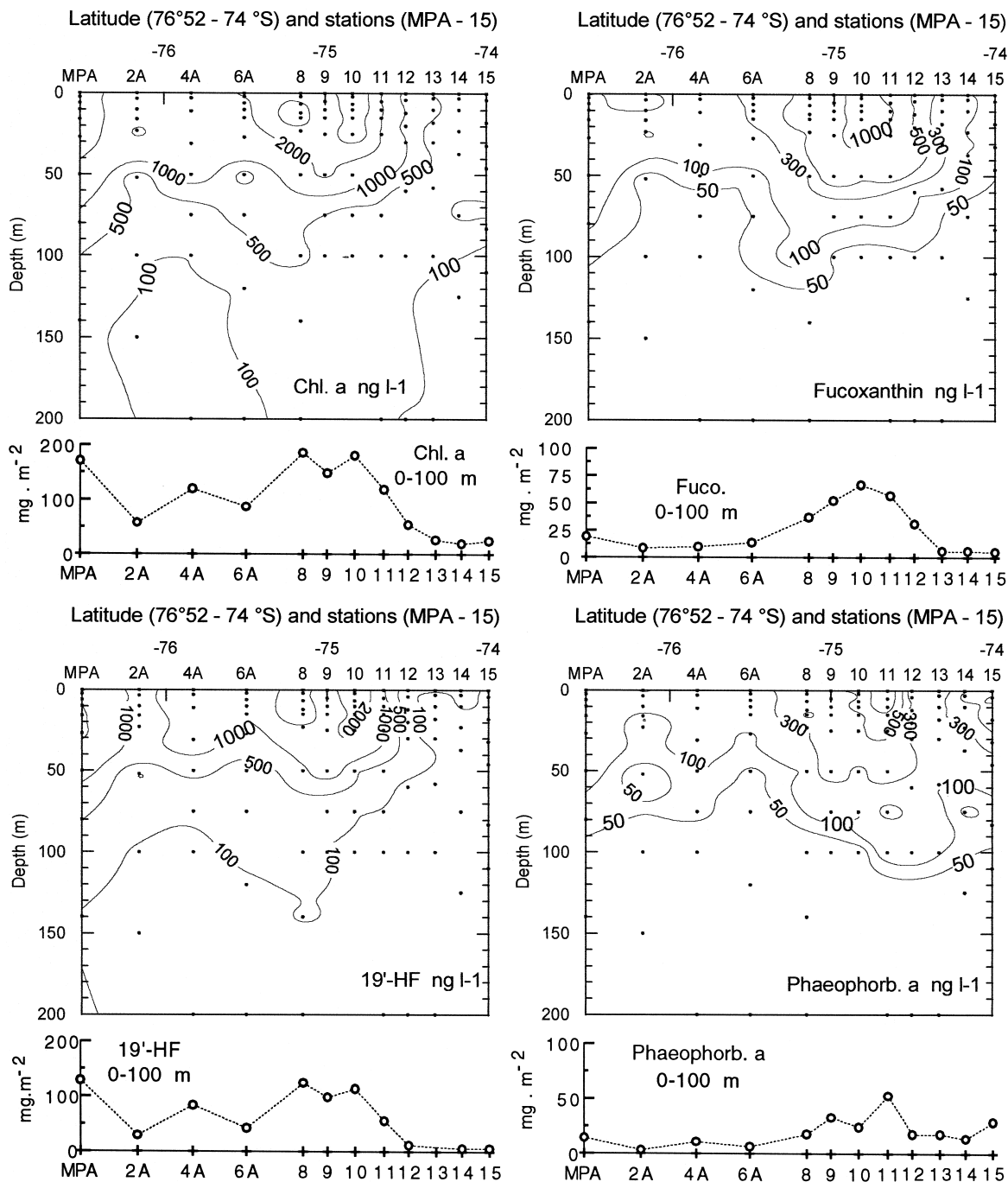


Fig. 5. Distribution of chl. *a*, fucoxanthin, 19'-HF and phaeophorbides *a* in the upper 200 m along transect 2 (ng l^{-1}). Integrated biomasses (0–100 m, mg m^{-2}) are shown below each section.

was reduced by about 65 μM within the surface mixed layer at station 25 (85 μM at 50 m, 17 μM at 5 m). At the same station, nitrate was reduced from ca. 30 μM below the pycnocline to < 10 μM at the surface.

3.2. South central Ross Sea: transect 2

Along transect 2, the area of investigation can be separated into three main regions based on the different ice conditions encountered: the polynya area (stations MPA-8), the marginal ice zone (stations 9–12) and the pack-ice zone (stations 13–15). This pattern was also reflected in the physical, chemical and biological variables focused on in this paper.

In the polynya area, the water column was mostly unstratified (Fig. 4), and its structure reflected a strong vertical mixing, as emphasized by the very low value of the average E_{max} ($6 \text{ m}^{-1} \times 1000$). Within the marginal ice zone, stratification increased slightly (average E_{max} of $8.5 \text{ m}^{-1} \times 1000$), as a result of a small decrease in surface salinity (less than 0.1% reduction in salinity, data from Russo et al., 1997). Further north, below the pack-ice, the water column reflected a typical homogeneous winter structure.

Similar and moderate standing crops of phytoplankton were found in the polynya and in the ice-edge area (Fig. 5). The polynya had integrated values of chl. *a* ranging from 58 to 186 mg chl. *a* m^{-2} in the upper 100 m while the ice-edge area showed integrated chl. *a* from 55 to 181 mg chl. *a* m^{-2} . Significantly lower levels of chl. *a* (20–27 mg chl. *a* m^{-2}) characterized the pack-ice area.

Along transect 2, 19'-HF was the major contributor to total carotenoid abundance and showed concentrations higher than those of fucoxanthin. The distribution of 19'-HF exactly followed that of chl. *a*, indicating that prymnesiophytes, and *Phaeocystis* in particular, were present both throughout the polynya and the marginal ice zone (29–132 mg 19'-HF m^{-2} in the upper 100 m). The variation of 19'-HF across the polynya and the marginal ice zone did not show any particular tendency. However, 19'-HF exhibits a drastic decrease in the water under the ice, even though it was dominant in melting-ice region.

On the other hand, fucoxanthin, the pigment second in abundance after 19'-HF, was strictly coupled

to the marginal ice zone where it showed marked increases (31–67 mg m^{-2} in the upper 100 m) as compared to polynya and pack-ice stations (Fig. 5). The maxima of phaeophorbides *a*, used as grazing tracer, also occurred in the marginal ice zone, where diatoms were most abundant. In that area, an important fraction of phytoplankton production appears to be transferred to higher trophic levels through herbivores, in particular through krill that were present in extremely high concentrations ($\approx 29 \text{ tons km}^{-2}$ at station 11; Azzali, personal communication).

During early spring, nitrate + nitrite and silicate concentrations in the south central Ross Sea were very high (Fig. 4). Ambient concentrations in the 100 m upper layer ranged from 24.7 to 32.0 μM for nitrate + nitrite and from 71.0 to 84.9 μM for silicate. The overall nutrient spatial variation was small, with slightly lower concentrations at the ice edge and on the northern side of the transect, below the pack-ice, implying the bloom had not existed very long.

4. Discussion

The range in pigment concentrations we report for transects 1 and 2 confirms the presence of substantial gradients in phytoplankton biomass and species distribution within the western and south central Ross Sea. The distributions of phytoplankton seem to be largely controlled by hydrological structure and water column stratification, which are themselves dependent on the mechanisms that govern the concentration of sea ice within the Ross Sea.

In the western Ross Sea, east of Victoria Land and Terra Nova Bay, the stratification of the water column results primarily from the input of low-salinity meltwater, most likely derived from sea ice which melts near the coast and from coastal glaciers (transect 1). The highest phytoplankton concentrations observed in this study were tightly coupled to the region of meltwater influence and were dominated by diatoms, as indicated by the elevated fucoxanthin concentrations. Typically, *Fragilariopsis curta* is the most abundant species in the sediment record of the western Ross Sea over the past 18 000 years (Kellogg and Truesdale, 1979) and dominates the diatom assemblage of other ice-edge blooms reported for the western Ross Sea (e.g. Wilson et al., 1986; DiTullio

and Smith, 1995). Consequently, its dominance within the ice-edge bloom we studied is assumed.

The overall spatial extent and biomass levels of the bloom we observed were similar to previous reported field observations dealing with summer conditions in the western Ross Sea. Our data suggest the annual occurrence of an intense diatom bloom associated with the coastal ice-edge region and allow us to accurately describe its spatial and temporal characteristics. Synthesis of available information (Table 2) suggests that a diatom-dominated ice-edge bloom extends off the coast of Victoria Land from 72°30'S to 77°S, within 100–250 km from the coastal ice edge and persists at least from early January to late February. However, pronounced nitrate and silicate depletion observed by early January within the high biomass core of our transect suggests that bloom initiation takes place much earlier in the season. This assumption is confirmed by satellite images, which reveal that substantial chl. *a* concentrations exist by mid-December in Terra Nova Bay (Arrigo and McClain, 1994). Although it is difficult to assign a time frame for a process controlled by physical conditions, it seems reasonable to infer that the diatom ice-edge bloom of the western Ross Sea persists on the order of 2.5–3 months. Although this estimate involves a number of uncertainties, it allows an appreciation of the temporal pattern of the bloom based on field observations and emphasizes its potential major role in the functioning of the pelagic ecosystem of the Ross Sea.

The only other carotenoid pigment detected in significant concentration within the area of meltwater influence was 19'-HF, used as marker for prymnesiophytes. The presence of 19'-HF could be attributable to *Phaeocystis*, whose presence in relatively small numbers ($60\text{--}170 \times 10^3 \text{ cells l}^{-1}$) was reported for Terra Nova Bay in January 1990 (Andreoli et al., 1993). The shift between the vertical distributions of fucoxanthin and 19'-HF suggests that 19'-HF containing cells have superior photoadaptive properties, as emphasized by Palmisano et al. (1986), and are able to survive at very low irradiances. For instance, at station 22, maximum of 19'-HF concentration was situated below the depth of 0.1% of light penetration.

Outside of the diatom-dominated ice-edge bloom, chl. *a* concentrations were markedly lower until

approximately 400 km seaward of the coast, where a secondary, less intense, chl. *a* maximum was detected in the open water. The open water chl. *a* maximum was different in its pigment composition from the diatom-dominated ice-edge bloom. It contained fucoxanthin and 19'-HF in similar proportions, indicating a mixed community of diatoms and prymnesiophytes. These observations coincide with those reported for the south eastern Ross Sea (76°30'S, 175–180°E) where a secondary chl. *a* maximum was found in late January 1990, 2–4 weeks after our transect (Nelson et al., 1991). The species composition within this area of moderate phytoplankton biomass was a mixed assemblage of *Phaeocystis* and numerous diatom species, with *Corethron cryophilum* and a *Chaetoceros* species the major contributors to the diatom biomass (Leventer unpublished data in Nelson and Tréguer, 1992).

The distribution of phaeophorbides *a*, in relation to chl. *a*, indicated that zooplankton grazing and phytoplankton biomass were tightly coupled. Within the diatom-dominated ice-edge bloom, grazing pressure significantly reduced the diatom biomass and transferred a sustained part of algal material to the herbivore trophic level. The most abundant mesozooplanktonic grazers were the thecosome pteropods *Limacina helecina* and copepods (Hecq et al., 1992). Adult and juvenile euphausiids were also observed. Grazing of phytoplankton was maximum in the central part of the bloom, while stations situated closer to the ice-edge were characterized by less grazed and probably younger diatoms based on pigment distributions. Thus, it appears that the stabilization of the upper layer of the water column associated with the receding ice-edge of the western Ross Sea favors diatom growth and accumulation. This is exploited by a classical food web where large herbivorous zooplankton provide the major link to larger animals and play an important role in regulating algal biomass. Moreover, the long duration of this phenomenon must influence substantially the fluxes of biogenic carbon and silica towards apex predators and deep waters.

The physical environment and the water column structure observed in the south central Ross Sea differ markedly from those observed in the western Ross Sea. Physical data along transect 2 demonstrate that very little meltwater had been introduced into

Table 2
Parameters characteristics of the ice-edge blooms of the western Ross Sea

Latitude	Period	Spatial extension of the bloom	Dominant phytoplankton	Pigment concentration within the ice-edge bloom	Pigment concentration outside the ice-edge bloom	Pigment concentration, average along the transect, including non-blooming area	Reference
72°30'S	12 January–05 February 1990	within the coastal region	Diatoms: <i>Fragilariopsis curta</i> , <i>Fragilariopsis cylindrus</i> , <i>Chaetoceros</i> spp. and <i>Corethron cryophilum</i>	3.7 mg chl. $a\ m^{-3}$ (maximum concentration)	–	–	Smith et al. (1996)
72°30'S	05–28 February 1992	within 150 km of the coast	Diatoms	2.4 mg chl. $a\ m^{-3}$ (maximum concentration)	–	0.61 mg chl. $a\ m^{-3}$	DiTullio and Smith (1995), Smith et al. (1996)
75°S–166°E (Terra Nova Bay) CZCS	10 December 1978–19 February 1979 16 January 1979	> 8000 km ²		1–10 mg m^{-3}	–	–	Arrigo and McClain (1994)
75°S	01–06 January 1990	220 km from the ice edge	Diatoms	$\geq 10\ mg\ m^{-3}$	–	–	This study
75°S	05–28 February 1992	within 150 km of the coast	Diatoms	6.76 mg chl. $a\ m^{-3}$ (maximum concentration) 129–358 mg chl. $a\ m^{-2}$ (0–100 m)	61–115 mg chl. $a\ m^{-2}$ (0–100 m)	2.10 mg chl. $a\ m^{-3}$ (0–100 m)	DiTullio and Smith (1995), Smith et al. (1996)
75°S	05–28 February 1992	within 150 km of the coast	Diatoms	3.1 mg chl. $a\ m^{-3}$ (maximum concentration)	–	2.15 mg chl. $a\ m^{-3}$	DiTullio and Smith (1995), Smith et al. (1996)
76°30'S	13 January–05 February 1990	100–150 km from the ice edge	Diatoms: <i>F. curta</i> (80–90% of the cells), <i>F. cylindrus</i> and <i>Fragilariopsis closterium</i>	11.8 mg chl. $a\ m^{-3}$ (maximum concentration)	–	–	Nelson et al. (1991), Nelson and Tréguer (1992), Smith et al. (1996)
76°30'S	05–28 February 1992	within 250 km of the coast	Diatoms	4.8 mg chl. $a\ m^{-3}$ (maximum concentration)	–	1.93 mg chl. $a\ m^{-3}$	DiTullio and Smith (1995), Smith et al. (1996)
76–77°S	January–February 1983	200–250 km from the ice edge	Diatoms: <i>F. curta</i> (70–80% of the cells) and <i>F. closterium</i> (5–20% of the cells)	146–322 mg chl. $a\ m^{-2}$ (0–150 m)	63–107 mg chl. $a\ m^{-2}$ (0–150 m)	–	Smith and Nelson (1985), Wilson et al. (1986)

All transects were normal to the coastal ice edge. See maps showing sampling locations in the original papers for longitudes.

the surface layer, even in the marginal ice zone, as referred to also by Smith and Gordon (1997). These observations suggest that direct melting plays only a minor role in the formation and opening of the Ross Sea polynya north of the Ross Ice Shelf. This hypothesis seems supported by the findings of Arrigo et al. (1998) who demonstrate that the mechanisms of the Ross Sea polynya formation are controlled mainly by air temperature in winter, which determine sea ice thickness and integrity. Polynya formation begins only when the temperature rises and the sea ice increases in brine volume, allowing sea ice breakup. Once ice breakup has begun, a set of complex processes interact to govern the concentration within the Ross Sea polynya, including the influence of surface currents and wind stress on sea ice distribution (Arrigo et al., 1998). With the opening of the polynya, the ice-free area is propagating from the south to the north until the beginning of January when the polynya becomes contiguous with the rest of the Ross Sea (Arrigo and McClain, 1994; Hecq et al., 1999).

As a consequence of these mechanisms of ice retreat, the water-column structure of the south central Ross Sea polynya is characterized by a relatively deep mixed layer, a low stability index, and a quite homogenous nutrient distribution. These conditions favor the presence of a bloom dominated by *Phaeocystis*, both in the polynya area and often in the weakly stratified marginal ice zone. *Phaeocystis* dominate in the south central Ross Sea probably because of their ability to maintain near-maximal photosynthetic rates at much lower irradiance levels than can diatoms (Leventer and Dunbar, 1996; Arrigo et al., 1999). By mid to late November, the latitudinal extension of the *Phaeocystis* bloom covered at least the area of the south central Ross Sea between 76°30'S and 74°50'S (transect 2). Complementary informations are provided by Smith and Gordon (1997) who observed *Phaeocystis* dominance at the same period of the same year along a longitudinal transect perpendicular to the Victoria Land coast at 76°30'S. In both cruises, nutrients and chl. *a* concentrations exhibited similar distributions. These results clearly indicate that *Phaeocystis* blooms in early spring in the Ross Sea polynya, when it can outcompete other species in the unstratified or poorly stratified water column.

At the northern limit of the polynya, fucoxanthin concentrations were significantly higher in close proximity to the retreating ice edge than for the open water region where ice had disappeared for some time. A diatom bloom was confined to the slightly stratified area of the marginal ice zone and overlapped with the *Phaeocystis* bloom. However, the spatial extension the diatom-rich band of the south central Ross Sea was quite narrow (ca. 30 km), corresponding with the reduced width of the slightly stratified marginal ice zone. Furthermore, fucoxanthin concentrations in the marginal ice zone of the polynya were approximately three times lower than within the diatom bloom observed in the western Ross Sea.

In spite of its reduced geographical extent, the marginal ice zone of the south central Ross Sea was an area of increased transformation of chl. *a*, mainly through grazing activity as suggested by the greater phaeophorbide levels. The degradation of the algal material appeared to be due to grazing pressure by various types of herbivorous zooplankton, among them the very large amounts of krill. These krill contributed to a total disappearance of the biomass of bloom-forming phytoplankton within 2 weeks (Hecq et al., 1999). Moreover, the diatom-krill assemblage characterizing the marginal ice zone of the polynya (Hecq et al., 1999) attracted remarkable populations of birds and Minke whales in a period of early production when diatoms are scarce in other areas.

To examine the relationship between water column stratification (itself depending on the mechanism of ice retreat) and diatom or *Phaeocystis* dominance, we plotted E_{\max} against integrated fucoxanthin and 19'-HF for each station of transects 1 and 2 (Fig. 6). The depth of integration $Z(L)$ was calculated according to Catalano et al. (1997), assumed to be the depth of the base of the pycnocline. The maximum observed values of integrated 19'-HF were observed in stations with very low E_{\max} ($< 10 \text{ m}^{-1} \times 1000$) corroborating the hypothesis that *Phaeocystis* are well adapted to a mixed water column (Fig. 6A). These values correspond to the polynya and marginal ice-zone stations of transect 2. However, a low E_{\max} does not necessarily imply a *Phaeocystis* bloom, as shown for the pack-ice stations of transect 2. In this case, very low irradiance below the pack

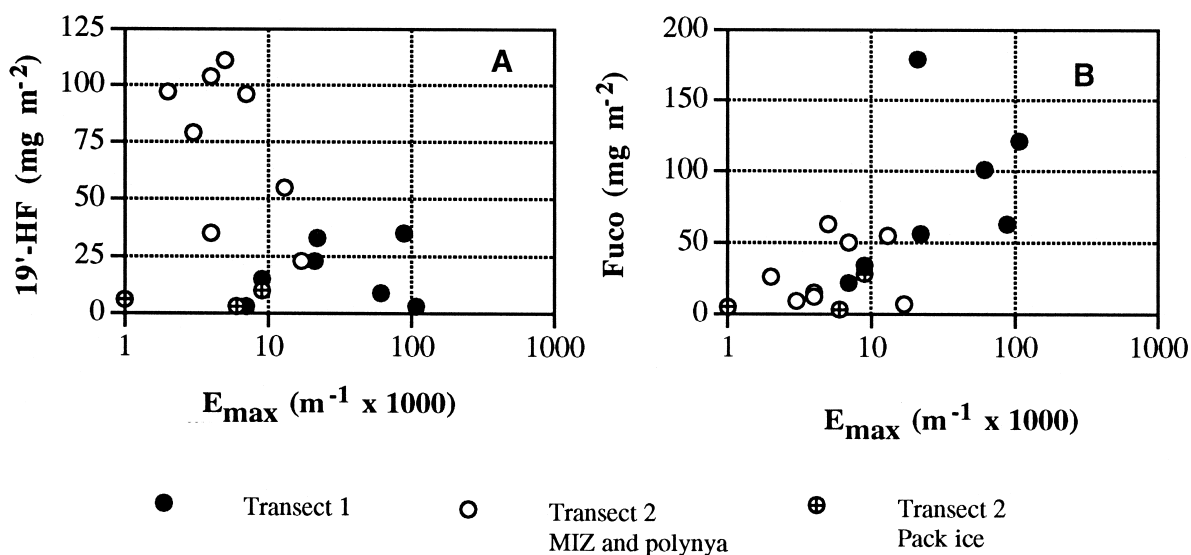


Fig. 6. Maximum vertical stability E_{\max} ($\text{m}^{-1} \times 1000$) vs. integrated 19'-HF (6A, mg m^{-2}) and fucoxanthin (6B, mg m^{-2}) for transects 1 and 2. Depth of integration $Z(L)$ was calculated according to Catalano et al. (1997).

presumably prevents *Phaeocystis* growth. On the other hand, diatom abundance showed a positive correlation with water column stability (Fig. 6B). Increasing water stability apparently favored the growth and accumulation of diatom standing crops and allowed them to adapt to a particular light regime.

Recently, evidence of seasonal iron limitation in the Ross Sea provided complementary information on the factors controlling biomass and species distribution in Antarctic shelf waters. Sedwick et al. (2000) showed that diatoms bloom only in the ice-edge regions, where both light and iron, supplied from melting sea ice, are abundant. In the unstratified waters, *Phaeocystis* dominated the algal community during spring and early summer in iron-replete conditions (> 1 nM dissolved Fe), as a result of iron supply from upwelled bottom waters. Later in the season, very low iron concentrations in the ice-free waters (< 0.2 nM dissolved Fe) limit both *Phaeocystis* and diatom growth.

In summary, it appears that the mechanisms of ice retreat within the Ross Sea (melting in the western Ross Sea and ice breakup and wind stress in the south central Ross Sea) control the water column structure, its stability characteristics and its iron contents. Large-scale melting, like in the western Ross

Sea, induces a highly stratified water column and allows the development of an intense diatom bloom associated with the iron-enriched coastal ice-edge region. On the contrary, in the south central Ross Sea, the processes of polynya formation result in relatively deep mixing and weakly stratified waters. *Phaeocystis*, as opposed to diatoms, appear to be better adapted to a less stable water column and bloom very early in spring in the polynya and the associated marginal ice zone. In addition, within the slightly stratified area of the marginal ice zone, at the northern limit of the polynya, a moderate diatom bloom overlaps with *Phaeocystis*. These typical patterns of phytoplankton distribution within the Ross Sea illustrate the importance of hydrodynamic processes of vertical stabilization which determine largely the dominance of diatom or *Phaeocystis* assemblages in Antarctic shelf waters.

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