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Phytoplankton biomass in an Antarctic coastal environment during stable water conditions – implications for the iron limitation theory

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ABSTRACT: The summer plankton community of Admiralty Bay (King George Is.) was studied in February 1987 under stable water column conditions which developed inside the bay after an unusually long period of predominant moderate to low wind speeds. The bay contained Fe in non-limiting concentrations, and the hypothesis was tested that Fe enrichment in natural environments would increase phytoplankton biomass. The phytoplankton was numerically dominated by nanoflagellates and small pennate diatoms. The protozoans were dominated by tintinnids and heterotrophic dinoflagellates, mainly *Gymnodinium* spp. Although the light/nutrient regime was optimum for autotrophic growth, the grazing pressure of microzooplankton precluded phytoplankton biomass accumulation, maintaining low chlorophyll *a* concentrations throughout the whole bay area during the 7 d of survey. The overall conclusion is that Fe enrichment of natural environments dominated by the microbial network may not result in high algal biomass.

INTRODUCTION

In recent years, a potentially stimulating effect of iron on the growth rate of phytoplankton in nutrient-rich/low-biomass areas such as the North Pacific and Southern Ocean has been demonstrated using bottle experiments (Coale 1988, Martin & Fitzwater 1988, De Baar et al. 1990, Martin et al. 1990). Iron addition is also said to favour the dominance of large diatoms (Hudson & Morel 1990). Large-scale fertilization with iron in the Southern Ocean has hence been proposed as a possible mechanism for increasing oceanic primary production, transferring more fixed carbon to the deep sea and ultimately reducing atmospheric carbon dioxide levels (Martin et al. 1990).

The evidence supporting this so called 'iron hypothesis' was critically reviewed at a recent meeting (Anonymous 1991) when the role of other biomass-limiting factors, such as grazing, were considered and a series of recommendations formulated concerning the implications of the 'iron hypothesis'. Pilot experiments were proposed in order to test the stimulation of iron under natural conditions and predict the ecological consequences of large scale iron-enrichments in the Southern Ocean.

One of the reasons why the iron hypothesis has generated so much controversy is because the regions considered so far are open ocean sites where factors other than iron availability can be invoked to explain low phytoplankton biomass in the presence of high nutrient concentrations. For instance, the low-grazing and highly stable (non-light-limited) regime inside enclosure experiments, typical of highly sheltered areas during the early spring-bloom periods, do not occur in the deeply mixed open ocean waters used to test the effect of iron on phytoplankton development.

In this paper I draw attention to a region – the coastal and shelf waters surrounding the Antarctic Continent – which can provide insight into the iron question. Since shelf waters contain iron above limiting levels for phytoplankton growth (Martin et al. 1990), they should support large phytoplankton blooms during stable periods. Indeed, in topographically protected areas along the Antarctic Peninsula, e.g. Deception Island and Gerlache Strait, such blooms have been reported for several years (Burkholder & Sieburth 1961, Holm-Hansen & Mitchell 1991), although they do not occur throughout the shelf regions.

Here I present the results of an investigation conducted in Admiralty Bay, King George Islands, during February 1987. An unusual long period of moderate to low wind speeds allowed stabilization of the upper water column inside Admiralty Bay and in adjacent open waters of the Bransfield Strait for almost 2 wk. Thus, the light/nutrient regime encountered by the natural phytoplankton population in the euphotic zone of the bay should have been comparable to those of bottle experiments used to test the potential effect of iron on the development of phytoplankton populations, with the advantage that the natural population of grazers was maintained. In addition, such conditions also simulate the pilot experiments proposed for testing the ecological consequences of iron fertilization in the Southern Ocean (Anonymous 1991), except that artificial enrichment with iron was not necessary because natural levels of iron in waters inside the bay, as well as in Bransfield Strait, must have been above limiting concentrations (Martin et al. 1990).

The present investigation provides evidence to predict final phytoplankton biomass and species composition in an iron-rich Antarctic coastal habitat after a long stable period. The objective was to show that grazing pressure can be the sole biomass-limiting factor in natural environments, despite large-scale enrichment with iron.

STUDY AREA

Admiralty Bay (Lat. 62° 03′ to 12′ S; Long. 58° 18′ to 38′ W) is the largest embayment on King George Island, South Shetland Archipelago. It has fjord-like geomorphologic features, with an area of 131 km^2 and approximately 18 km^3 of water (Rakusa-Suszczewski 1980). The main entrance is a deep channel with a maximum depth of 530 m, through which water exchange with the Bransfield Strait takes place via tidal currents and wind-induced watermass transport.

Chlorophyll *a* (chl *a*) concentrations during summer are usually below 0.5 $\mu g\ l^{-1}$, and frequently even lower than in the open waters of the Bransfield Strait (Rakuza-Suszczewski 1980, Lipski 1987). This has been attributed to westerly and northerly katabatic winds, which are more frequent during warmer seasons (Nowosielski 1980, Pruszak 1980). These winds drive the surface layers towards the outer bay generating turbulence in the form of upwelling in the inner inlets. Therefore, an autochthonous plankton community may develop inside the bay only when water exchanges with the Bransfield Strait are delayed during stable meteorological conditions.

MATERIAL AND METHODS

A survey of hydrography and plankton was carried out in Admiralty Bay aboard the RV 'Prof. Besnard' (São Paulo University), between 13 and 19 February 1987, within the framework of the Fifth Brazilian Expedition to the Antarctic.

Stns 1 to 18 (Fig. 1) were all (except for Stn 5A) sampled from 13 to 18 February 1987. Water was collected with Nansen bottles down to 100 m for analyses of chl *a*. (Samples for microscopic analyses were not obtained.)

Stns 6, 10, 13 & 17 were sampled again on 19 February, as well as Stn 5A. Secchi disk readings were taken prior to sampling and the euphotic zone was estimated using the empirical equation suggested by Gieskes et al. (1989). Depth profiles of temperature and salinity were obtained respectively using reversing thermometers and induction salinometers. Water samples were again collected with Nansen bottles from 0, 10, 25, 50, 75, 100, 150 and 200 m for chl *a*, nutrient and microscopic analyses.

The nutrients, nitrate (+nitrite)-N, phosphate-P and silicate-Si were determined photometrically according to Strickland & Parsons (1972). For chl *a* determina-

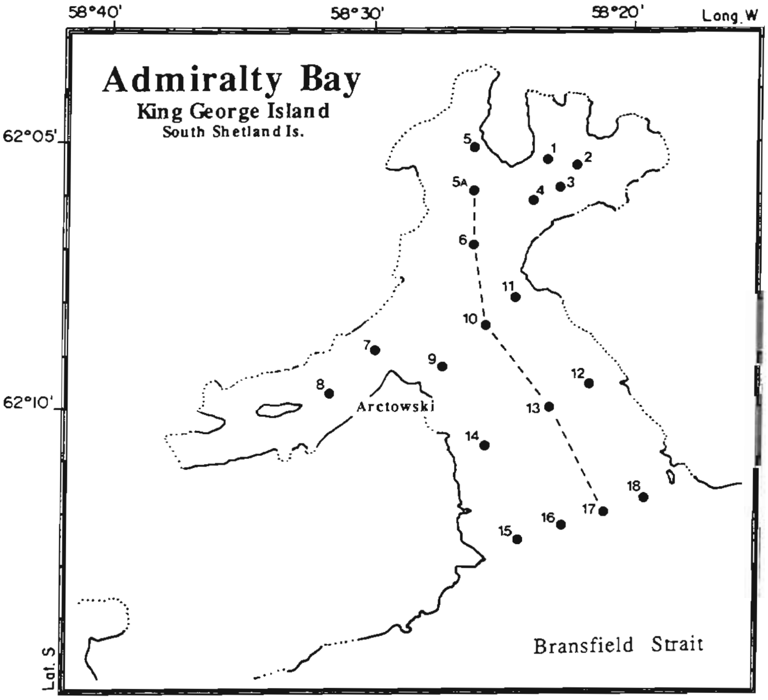

Fig. 1. Admiralty Bay, King George Is., showing positions of stations sampled on 13 to 18 February 1987 The transect formed by Stns 5A to 17 was sampled on 19 February

tions 200 ml of water were filtered onto Whatmann GF/F filters and the fluorescence of acetone extracts was measured with a Turner 111 fluorometer, following the procedures recommended by Evans & O'Reilly (1983).

Aliquots of 50 ml were taken from the Nansen bottles and preserved with 0.4 % (final concentration) neutral formaline solution for Utermöhl (1958) analyses. Prior to sedimentation they were stained with Bengal Rose to better distinguish organic from inorganic material. A Zeiss inverted microscope was used for counting the total micro-size (> 20 µm) cells in a half chamber area (alternate transects), under phase contrast with a magnification of ×130. A minimum of 100 nano-size cells were counted in cross diameter transects at magnification ×800, within size categories of 3-6, 6-12 and 12-20 µm. Net samples were sometimes collected for checking the general microplankton composition.

Meteorological data was obtained from the Polish Institute of Meteorology and Water Management (Arctowski Station) and from the ship's cruise data files (unpubl.).

RESULTS

Hydrography

Calm weather conditions prevailed during the first half of February, with moderate to low daily averages in wind speed (0 to 6 m s^{-1}), alternating from directions NNW to ENE. On 15 February, daily wind speed increased briefly to 17.8 m s^{-1} but decreased to moderate levels between 4 and 7.5 m s^{-1} until 19 February. The wind regime did not cause strong turbulence in the surface water, and did not affect the physically stable conditions that developed during the first 15 d of February.

The depth profiles of physico-chemical parameters, chl *a* and cell counts obtained at Stns 5A, 6, 10, 13 & 17 provided an average picture of these parameters for the main axis of the bay on 19 February.

The vertical distributions of sigma-T along the transect indicated an upper mixed layer of 25 to 30 m (Fig. 2). Surface temperature reached a maximum of 0.91 °C and salinity dropped to a minimum of 33.7 ppt. The euphotic layer was approximately 40 m thick. Nutrient concentrations were very high at the transect stations, nitrate (+nitrite) varying from 17.2 to 30.3 µM, phosphate from 0.88 to 2.08 µM and silicate from 46.0 to 71.7 µM. The patterns of nutrient depth distributions at these stations (Fig. 3) did not show significant differences between concentrations in upper euphotic and deeper aphotic layers. No significant depletion was detected in surface layers. Silicate concentrations were slightly lower in the euphotic zone and similar in all stations. Nitrate-N varied irregularly in the euphotic zone of all stations and tended to increase with depth. Phosphate-P profiles varied significantly between stations, decreasing towards the outer bay.

Chlorophyll *a*

Patterns of vertical distribution of chl *a* obtained in the whole bay between 13 and 18 February varied between stations (Fig. 4). Concentrations ranged from 0.1 to 1.5 µg l^{-1}, with peaks detected in surface and/or subsurface layers. Levels were normally between 0.5 and 1 µg l^{-1}, even at greater depths. Depth-integrated values

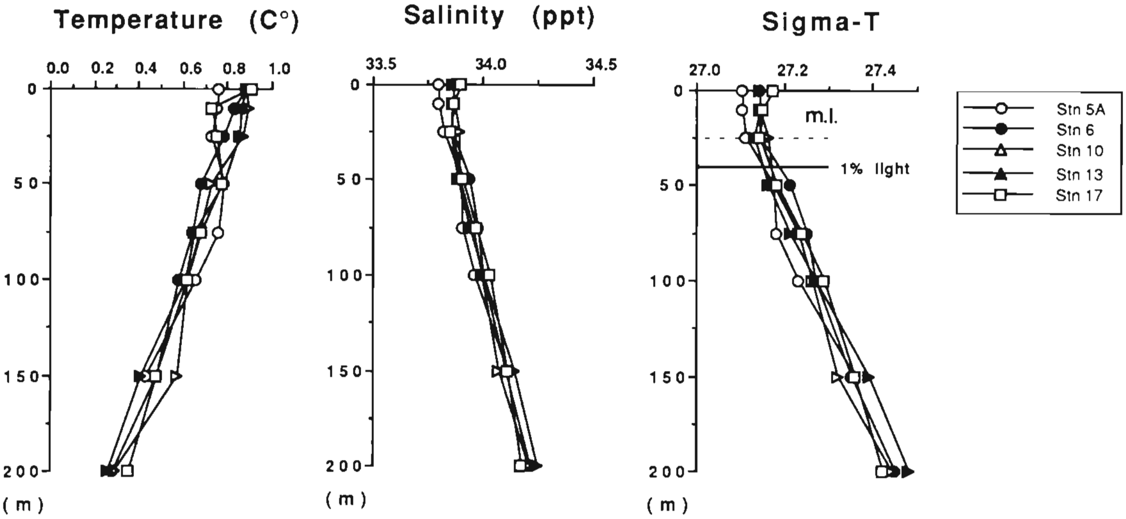

Fig. 2. Depth distributions of temperature, salinity and density (sigma-T) along the transect (Stns 5A to 17) surveyed on 19 February. The thickness of the upper mixed and euphotic layers is also indicated

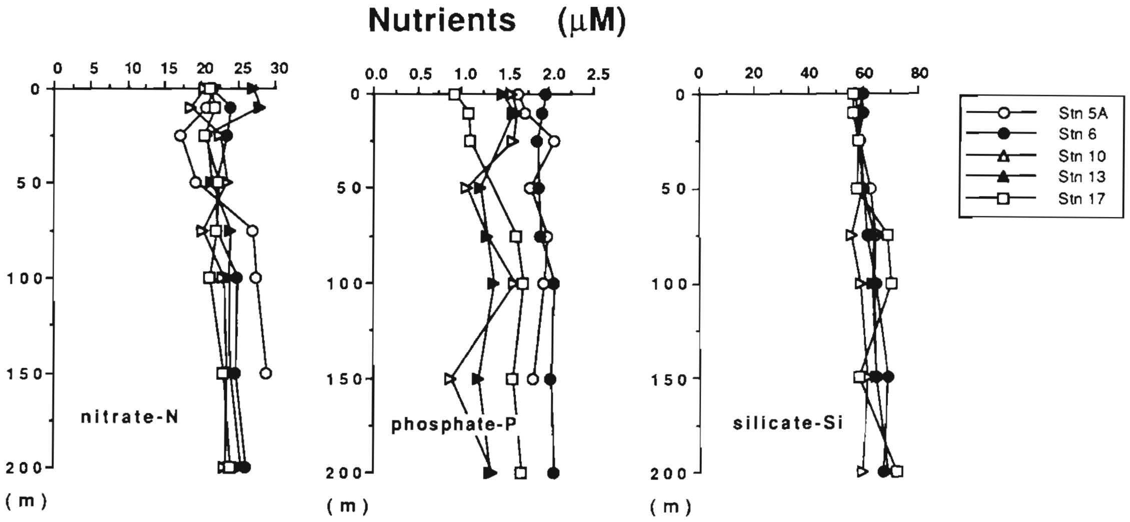

Fig. 3. Depth distributions of nutrients along the transect (Stns 5A to 17) surveyed on 19 February

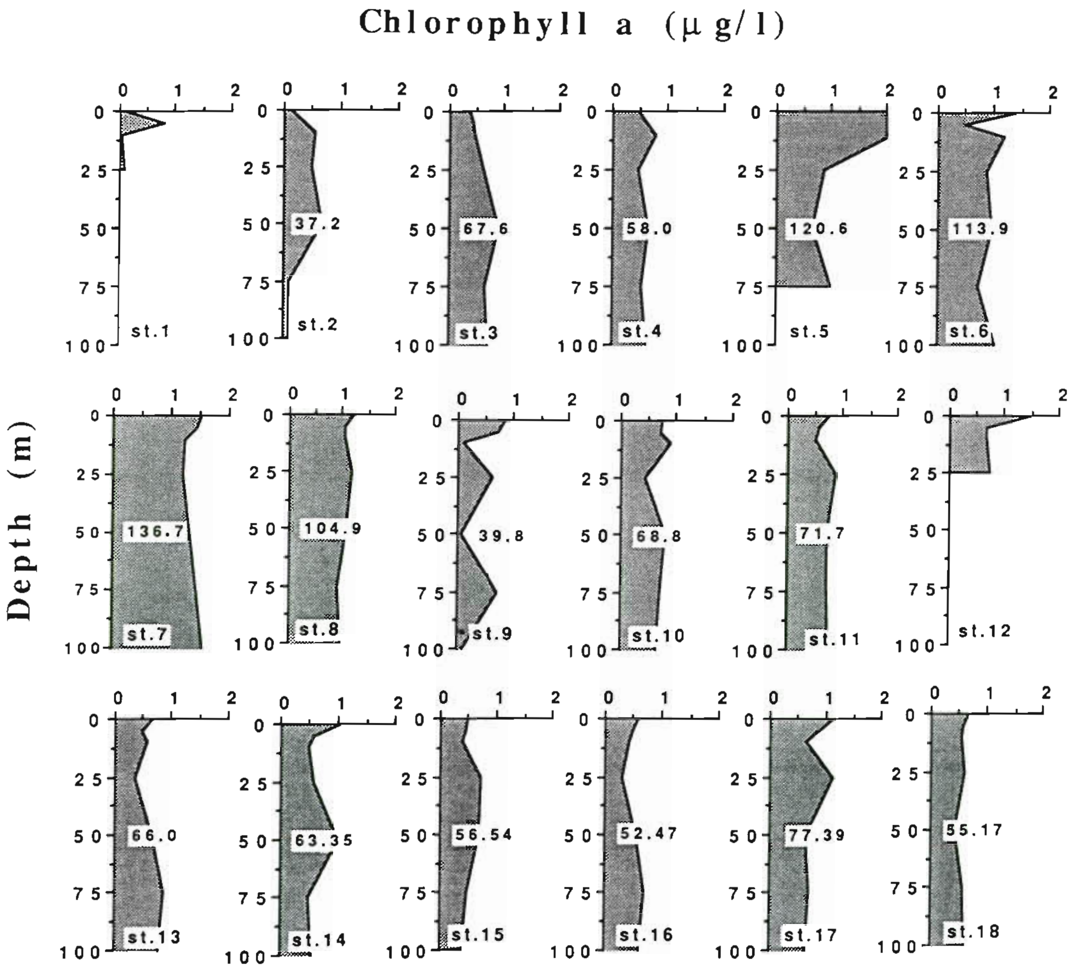

Fig. 4. Depth distributions of chl *a* at all stations in Admiralty Bay surveyed between 13 and 18 February 1987 Integrated values in mg m^{-2} are also given

over 100 m varied from 37.2 to 120.6 mg m^{-2}, with maxima at the inner Stns 5, 6, 7 & 8 in the Mackellar (northern) and Ezcurra (western) inlets. Chl *a* stocks along the deep channel area, i.e. the transect formed by Stns 5A to 17, were lower than 100 mg m^{-2}.

On 19 February, concentrations of chl *a* stocks along the longitudinal transect were still below 100 mg m^{-2} (integrated data not shown), varying from 0.28 to 1.13 µg l^{-1} (Fig. 5). Vertical distributions along the transect were more or less homogeneous throughout the euphotic zone, decreasing only slightly with depth. Over the 7 d of survey, with favourable weather conditions and high water stability, the stocks of chl *a* did not increase.

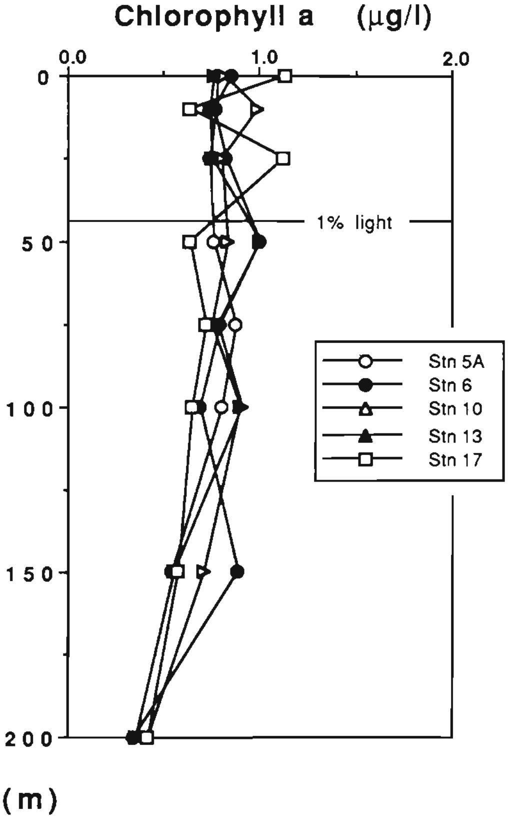

Fig. 5. Depth distributions of chl *a* along the transect (Stns 5A to 17) surveyed on 19 February. The 1 % light depth is also indicated

Nanoflagellates and monads

Cells of 3–6 and 6–12 µm size were abundant in the upper euphotic layers at all stations along the longitudinal profile, with densities ranging respectively from 100 to 550 × 10^3 and from 20 to 200 × 10^3 cells l^{-1}, respectively (Fig. 6). Monads and unidentified cells with either 1 or 2 flagella dominated the 3–6 µm size. Choanoflagellates (Craspedophyceae) were abundant within this size-class, with maximum densities of up to 46 × 10^3 cells l^{-1} (between 25 and 50 m at Stns 5A & 6). Cryptophytes dominated the 6–12 µm size category, followed by prasinophytes and *Prorocentrum antarcticum*. Cells between 12 and 20 µm were mostly dinoflagellates belonging to the genera *Gymnodinium*, *Amphidinium* and *Protoperidinium*. *Pyramimonas* sp. of 15 µm was also present but in lower densities.

Microflagellates

These were mostly represented by heterotrophic dinoflagellates dominated by *Gymnodinium* spp. of 20 to 30 µm size (concentrations up to 35 000 cells l^{-1}). *Gyrodinium glaciale*, *G. lachryma* and *Amphidinium hadai* followed in dominance with maximum densities of 3600, 1700 and 1700 cells l^{-1}, respectively. Patterns of depth distributions of all species showed higher concentrations in the subsurface levels of the euphotic zone, decreasing with depth (Fig. 7).

Diatoms

Nano-sized diatoms (< 20 µm) were dominated by *Nitzschia cylindrus* (valve diameter 5 µm), with concentrations ranging from 20 to 200 × 10^3 cells l^{-1}. They were concentrated between 10 and 25 m, decreasing with depth (Fig. 8). *Chaetoceros neglectum*, *Chaetoceros bulbosum* and *Chaetoceros criophilum* were always present but at cell concentrations 2 orders of magnitude less than *N. cylindrus*. Total diatoms of the micro-size class (> 20 µm) were irregularly distributed at stations along the profile, with concentrations ranging up to 15 000 cells l^{-1}. They concentrated mostly at subsurface levels, between 10 and 50 m. The dominant species were *Nitzschia curta*, *Porosira* sp., *Thalassiosira tumida*, *Odontella weissflogii*, *Eucampia antarctica*, *Rhizosolenia truncata* and *Corethron criophilum*.

Ciliates

The ciliated protozoans were dominated by tintinnids, mostly concentrated in euphotic layers (Fig. 9). The '*Coxliella*' form was relatively abundant, with densities reaching up to 3520 cells l^{-1}. It was concentrated in the upper 25 m, decreasing sharply downwards. *Amphorides laackmanni* was also abundant, reaching maximum concentrations (up to 1600 l^{-1}) in lower levels of the euphotic zone. Other tintinnids found included *Cymatocylis convallaria*, *C. drygalskii*, *Codonelopsis gaussi*, *C. balechi*, *Tintinnopsis bacillaria* and *Laackmanniella naviculaefera*. They oc-

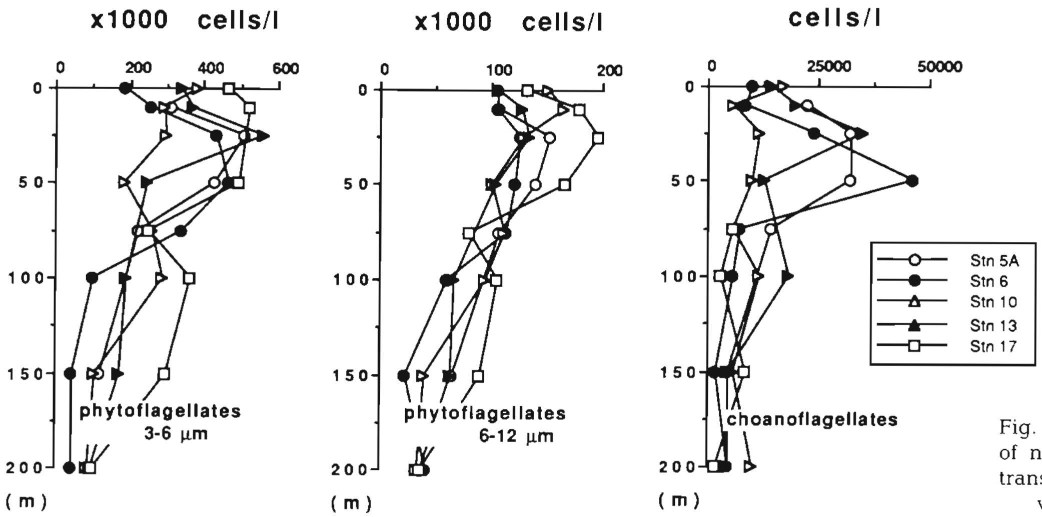

Fig. 6. Depth distributions of nanoflagellates along the transect (Stns 5A to 17) surveyed on 19 February

curred in all samples but at low densities. The aloricate species were also concentrated in surface euphotic layers with a maximum of 2240 l^{-1} at 10 m at Stn 5A. They were totally dominated by one unidentified species of *Strombidium* which was rarely observed beneath 75 m. Other aloricates were present but in relatively small amounts.

DISCUSSION

Hydrography and pelagic community structure

The physical environment inside the bay may be considered an extension of the hydrographic conditions on the northern shelves of the Bransfield Strait, modified by local processes (e.g. tides, melting of glaciers, resuspension of bottom sediments) during longer periods of water residence.

During the summer a typical plankton community with a regenerative character dominates around the Antarctic Continent (Hewes et al. 1985, Smetacek et al. 1990). Autotrophs are dominated by nano-size cells, usually flagellates, whilst the main herbivores are protozoans, especially ciliates and heterotrophic dinoflagellates (Hewes et al. 1985, Alder & Boltovskoy 1991, Nöthig et al. 1991). This 'microbial network' (*sensu* Smetacek et al. 1990) was found in the pelagial of Admiralty Bay during this investigation.

Since nitrate-based production represents a minor contribution in the late summer Antarctic regenerative systems (Olson 1980, Koike et al. 1986), nitrate decreased only slightly in the euphotic zone. Apart from ammonium regeneration in the pelagial, the pelagic

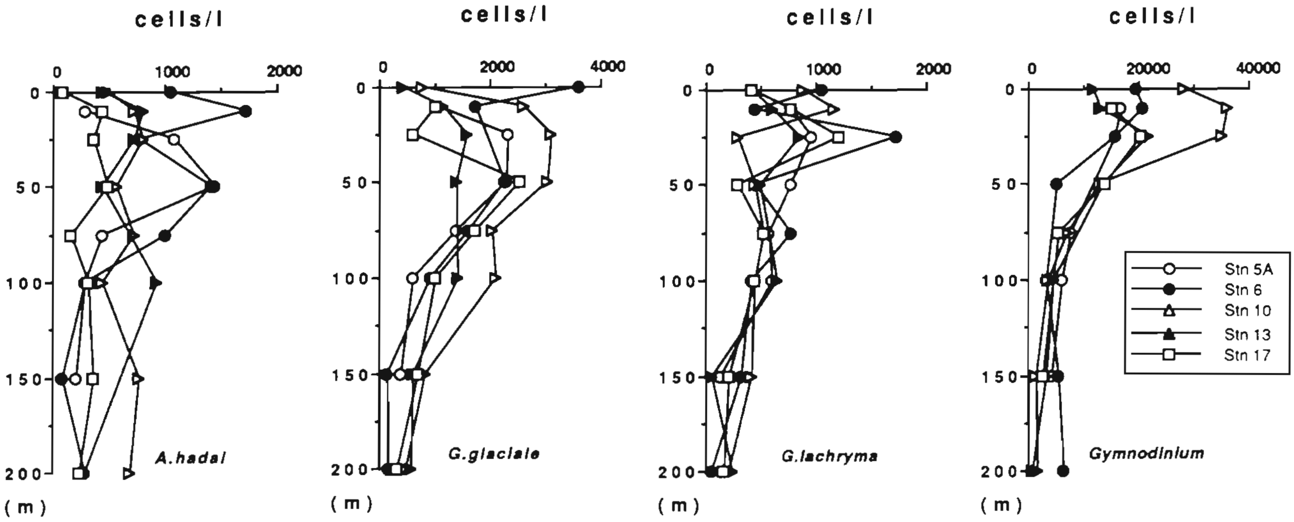

Fig. 7. As for Fig. 6, but for heterotrophic dinoflagellates

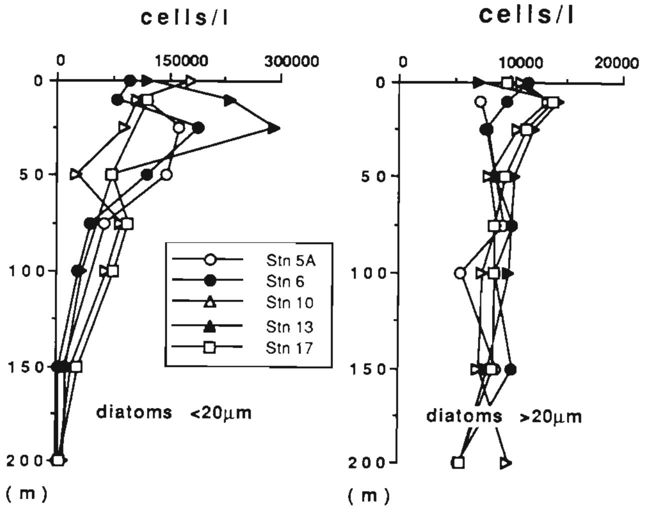

Fig. 8. As for Fig. 6, but for diatoms

community of Admiralty Bay is also supplied with considerable amounts of biogenic dissolved and particulate compounds derived from land or carried from benthic sources during turbulent periods (Dawson et al. 1985). Degradation of these substances contributes significantly to the pool of reduced nitrogen in the water column and should especially favour the smallest organisms of the nano-size category. Indeed, cells smaller than 12 µm, mostly represented by cryptophytes, prasinophytes and small diatoms, numerically dominated the autotrophs in the bay.

Nitzschia cylindrus was the dominant diatom in this size-fraction, however its contribution to the chl *a* biomass was insignificant. Assuming a reasonable carbon content per cell of 1 pg and a C:chl *a* ratio of 50 (Mitchell & Holm-Hansen 1991), the highest density of *N. cylindrus* recorded in this survey (300 000 cells l^{-1}; Stn 13, 25 m) contributed to less than 0.01 µg chl *a* l^{-1}. Large diatoms were present but in very low numbers and, therefore, they also did not contribute significantly to the chl *a* stock in the euphotic layer. Copepod nauplii were abundant during the survey period (M. Montú pers. comm.) and were certainly grazing on micro-size diatoms, maintaining the observed low cell densities (<15 000 cells l^{-1}). Hence, vertical distributions were irregular probably due to the larger variation inherent in the counting procedure.

Besides growth, the stable conditions in the bay allow the microheterotrophs (mainly dinoflagellates and tintinnids) to concentrate in the euphotic zone by swimming upwards (Hasle 1950, Heany & Eppley 1981, Levandowsky & Kaneta 1987). This was demonstrated in laboratory experiments showing that, in the absence of turbulence, they can cross pycnocline gradients and concentrate close to the surface (Jonsson 1989).

Grazing pressure

The phytoplankton growth model developed by Mitchell & Holm-Hansen (1991), with data from the RACER program, is able to predict the amount of phytoplankton biomass accumulation in relation to the extent of the upper mixed layer (UML). However, the effect of grazing pressure, particularly from microheterotrophs, was one of the major factors in their model affecting the predicted biomass. In other words, the higher are the loss terms due to grazing, the lower is the size of the maximum phytoplankton crop which can be achieved even in a very shallow UML. In the present investigation, the UML was not deeper than 25 m whilst the euphotic zone extended further to 40 m (Fig. 2). If one applies Mitchell & Holm-Hansen's model under these conditions, algal biomass should necessarily reach

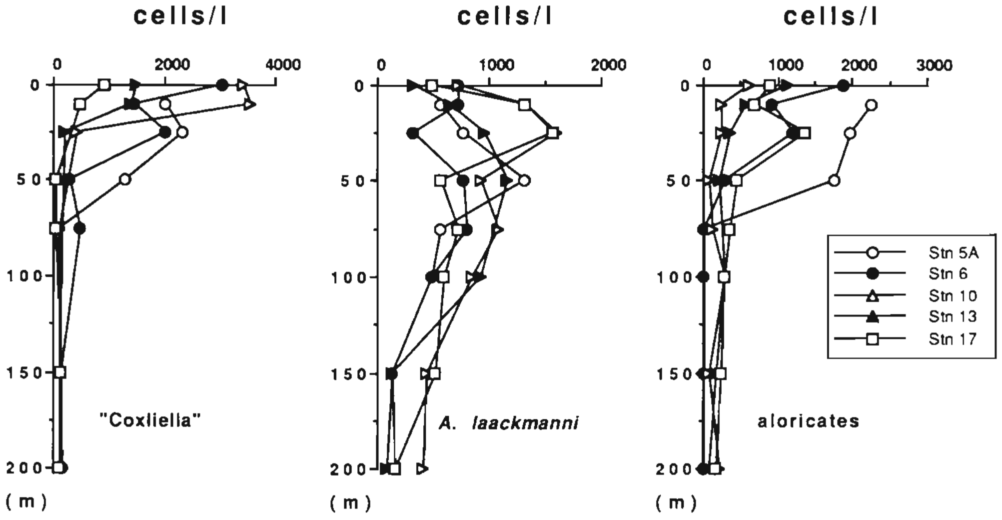

Fig. 9. As for Fig. 6, but for dominant ciliates

bloom levels if grazing pressure is insignificant (see Fig. 6 of Mitchell & Holm-Hansen 1991).

Considering the range of growth rates of phytoplankton in the Antarctic of 0.5 to 1 d^{-1} (Spies 1987, Sommer 1989), and an average chl *a* stock of 100 mg m^{-2} at the beginning of the survey, final chl *a* biomass after 7 d should reach values at least one order of magnitude higher. Nevertheless, the chl *a* stocks in the bay remained low in spite of the almost 2 wk of water stability, rarely exceeding 1 $\mu g\ l^{-1}$ throughout the euphotic layer (see Figs. 4 & 5).

There is a general consensus that, in quantitative terms, the microbial network tends towards a steady-state condition, in which gains in autotrophic biomass are balanced by losses due to grazing pressure by zooplankton (Smetacek et al. 1990). The grazing impact of heterotrophic dinoflagellates (the dominant microzooplankton in this study) on phytoplankton has been reported recently in Antarctic habitats (Nöthig & Bodungen 1989, Buck et al. 1990, Bjørnsen & Kuparinen 1991, Nöthig et al. 1991). They can prey on a wide variety of particle sizes and even on diatoms and ciliates of similar size to themselves (Gaines & Elbrächter 1987). The species observed in Admiralty Bay (*Gymnodinium* spp., *Amphidinium hadai, Gyrodinium glaciale* and *G. lachryma*) are common in the Antarctic (Hada 1970), and have been reported along the Antarctic Peninsula (Brandini & Kutner 1986, Hewes et al. 1990). Although they were described by Balech (1976) as autotrophs, Hewes et al. (1990) confirmed the lack of chloroplasts in *G. lachryma* and *A. hadai*, and González (pers. comm.) confirmed the ingestion of large diatoms by unarmoured dinoflagellates (including *G. lachryma*) in coastal waters off the South Shetland Islands. Observations of live material (net-samples) during the present investigation did not reveal the presence of chloroplasts inside the *Gymnodinium* spp., the dominant heterotrophic dinoflagellate during this survey.

Assuming the maximum carbon ingestion rate of a single gymnodinian cell as 6 pgC h^{-1} $cell^{-1}$ (= 0.14 ngC d^{-1} $cell^{-1}$) (Bjørnsen & Kuparinen 1991), and a carbon production rate of approximately 10 mgC m^{-3} d^{-1} estimated from investigations carried out in the bay and in waters of the Bransfield Strait (Teixeira et al. 1986, Domanov & Lipski 1990), the grazing impact of 20000 gymnodinians l^{-1} (the approximate average concentration found in this investigation; see Fig. 7) would remove 2.8 mgC m^{-3} d^{-1}, i.e. 28 % of the daily autotrophic carbon fixation. If grazing by ciliates is also considered, one may conclude that the daily carbon fixation is in balance or even insufficient to maintain the requirements of the total microzooplankton. In the latter case, the organisms may complete their daily diet with allochtonous land or benthic sources of organic carbon (Dawson et al. 1985).

These assumptions emphasize the magnitude of the grazing pressure by microheterotrophs on either living cells or detritus. Under these conditions, it is not surprising that phytoplankton biomass, expressed as chl *a*, did not increase in the 7 d of survey during which favourable growth condition prevailed.

CONCLUSIONS

Martin et al. (1990) found iron concentrations in coastal areas along the Gerlache Strait of 7 nM at the surface, i.e. far above the limiting range of 0.1 to 1 nM for phytoplankton growth reported in experimental work (Martin & Fitzwater 1988, De Baar et al. 1990). Therefore, the approximately 15 d of stable water column conditions in Admiralty Bay more or less resembles the environment inside iron-enriched bottles and should support high biomass and, according to Hudson & Morel (1990), the dominance of large diatoms. This was not however observed.

The results of this investigation show clearly that fertilization of natural environments with iron does not necessarily increase phytoplankton biomass, especially when most of the fixed carbon is cycled within a well-developed microbial network, as observed during late summer in Admiralty Bay and in most of the oceanic waters around the Antarctic. Buma et al. (1991) also found a rapid response of protozoan grazers to increasing phytoflagellate biomass stimulated by iron enrichment during spring when the pelagic system was in the process of developing a complex food web.

The overall conclusion is that iron enrichment *per se* is unlikely to result in substantially high algal biomass after long stable periods, at least when the microbial network is the dominant community and the grazer response of such a community is unchecked.

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