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Article

A Possible Explanation for the Dominance of Chlorophyll in Pico and Nano-size Fractions in the Waters Around the South Shetland Islands

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Abstract : Chl *a* abundance, Chl *a*-specific productivity and phytoplankton growth rate in each size fraction (pico, <2 μm; nano, 2-10 μm; micro, >10 μm) in the waters around the South Shetland Islands (Antarctic Peninsula Area) were analysed. Although Chl *a*-specific productivity and growth rate were highest in micro-size fractions, Chl *a* abundance was highest in pico-size fractions. Selective removal of nano- and micro-size phytoplankton especially by krill and salp grazing, but not limitation of phytoplankton growth, seemed to be the major reason to explain this miss match between productivity and abundance of the phytoplankton community.

Key words : chlorophyll concentration, primary productivity, size fraction, grazing pressure, antarctic krill, salp.

1. Introduction

It has been suggested that size fractionated measurements of phytoplankton are important for understanding the response of each fraction to environmental conditions (Malone 1980). Also, when assessing phytoplankton populations as food reservoirs, it is important to consider their size distribution (Villafane *et al.* 1993). During the last two decades, many studies related to the population of Antarctic phytoplankton were undertaken. They revealed that the populations are often dominated by pico and nano-size cells (e.g. Hewes *et al.* 1985). However, studies relating abundance to productivity of phytoplankton based on cell sizes, are still very limited in the Southern Ocean.

Weber and El-Sayed (1987) and Hosaka and Nemoto (1986) reported higher Chl *a*-specific productivity in micro size compared to pico- and nano-size fractions in the Indian Sector. In their cases, Chl *a* abundance also showed high values in micro-size fractions. On the other hand, Xiuren *et al.* (1996) reported both high Chl *a*-specific productivity and Chl *a* concentrations in pico-size fractions in the Atlantic Sector. In those studies, the size

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fraction showing the highest productivity seemed to result as the dominant size fractions of the Chl *a* abundance. However, Shiomoto *et al*. (1998) reported that although Chl *a* abundance in pico-size fraction was dominant, Chl *a*-specific productivity in pico-size fraction was not necessary higher than that of larger phytoplankton around the South Shetland Islands (Antarctic Peninsula area). In the last case, there was a major miss-mach between abundance and production.

The purpose of this study is to discuss the cause of this miss match, by performing statistical reanalysis of the data obtained in Shiomoto *et al*. (1998) and also by analysing results from dilution experiments performed in austral summer 2000 in the waters around the South Shetland Islands.

2. Materials and methods

Primary productivity

The measurements were conducted between December 1994 and February 1995 during the cruise of R/V Kaiyo-Maru (Fisheries Agency), off the northern coast of the South Shetland Islands. Four transect surveys (A, B, C, and D) were operated with approximately two weeks intervals (Fig. 1). Two stations of the first transect were moved to the east parallel to the bottom topography, because of the ice extension. Phytoplankton productivity was measured by simulated *in situ* methods using a ^{13}C-technique (Hama *et al*. 1983). Sea water samples were collected between 9:00 and 12:00 a.m. from four depth corresponding to 100, 23, 12, and 1 % light depths using an acid-cleaned plastic bucket or 30-l Niskin PVC sampler with a Teflon-coated steel spring. Water samples were sieved through a 330-μm mesh screen to remove large zooplankton. The incubation lasted for approximately 3 hours. Phytoplankton productivity in each size fraction such as pico-size (0.7 to 2.0 μm), nano-size (2.0 to 10 μm), and micro-size (10 to 330 μm) were measured by using glass fiber and membrane filters of different pore size. Methods in detail are described in Shiomoto *et al*. (1998).

Measurement of phytoplankton growth rate and grazing pressure using dilution method

Four experiments were conducted from late January to early February 2000 during the cruise of R/V Kaiyo-Maru in the vicinity of the South Shetland Islands (Fig. 1). Phytoplankton growth rate (μ) and microzooplankton grazing rates (g) were estimated using the dilution method of Landry and Hassett (1982). Growth and grazing rates were determined in pico-size (0.7 to 2.0 μm), nano-size (2.0 to 10 μm), and micro-size (10 to 330 μm) fractions following Tsuda and Kawaguchi (1998). Surface water was obtained with a plastic bucket and filtered through 330 μm to remove macrozooplankton. The prefiltered surface water was sequentally diluted with filtered seawater

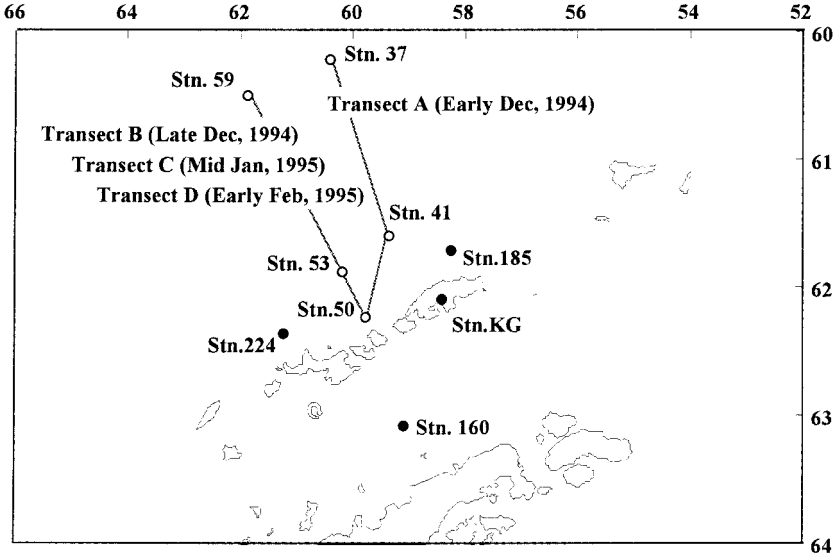

Fig. 1. Location of sampling stations in the waters around the South Shetland Islands. Open circles are the stations for primary productivity experiment in the 1994/95 cruise, and solid circles are the stations for dilution experiments in the 2000 cruise.

(GF/F). Then, a series of HCl prewashed polycarbonated bottles (1 *l*) were filled with the diluted water and incubated for 2 days in the deck aquarium with continuous flow of surface seawater. Chlorophyll concentration was used to monitor the phytoplankton abundance.

Environmental measuremnents

Salinity and temperature profiles were determined with CTD profiler (SBE911 plus, Seabird Electronics Inc.). Nutrient concentrations and size distribution of chlorophyll particles were determined at each station. Size fractionated (0.2-2.0, 2.0-10, 10-330 μm) Chl *a* concentrations were measured fluorometrically by the same procedure mentioned above. Nutrient concentrations were measured using an Auto Analyzer II (Technicon) by standard methods (Parsons *et al*. 1984).

Statistical analysis

Analyses of deviance were carried out for the phytoplankton productivity data, using a generalized linear model (GLM, S-Plus software package) with Chl *a* concentration or Chl *a*-specific productivity as dependent variables. Zone of the water mass, season, percent light depth, and size were used as categorical factors. Depth of mixing layer and temperature were used as continuous independent variables. Only main effects were estimated because there is only one observation per cell. Analyses of deviance were also carried out for the data from dilution method, using phytoplankton growth and grazing as dependent variables. Stations and size were used as categorical factors. A non parametric test (Mann-Whitney's U-test) (Zar 1996) was also performed to see any significant unbalance between phytoplankton growth rate and microzooplankton grazing.

3. Results

Overview of the environments at the stations for primary productivity

Analysis of the temperature and salinity profiles revealed that the stations may fall into three of six different water zones defined in Holm-Hansen *et al*. (1997) (Fig. 2). The oceanic stations (Stn. A-37, B-59, C-59, and D-59) fell into Zone 1 water, which is characterized by warm, low-salinity surface water, a strong subsurface temperature minimum, and T/S maximum near 500 m. The stations in the shelf break (Stns A-53, B-53, C-53, and D-53) fell into Zone 3, which is characterized by broad temperature minimum. The on shelf stations (Stn. A-50, B-50, C-50,

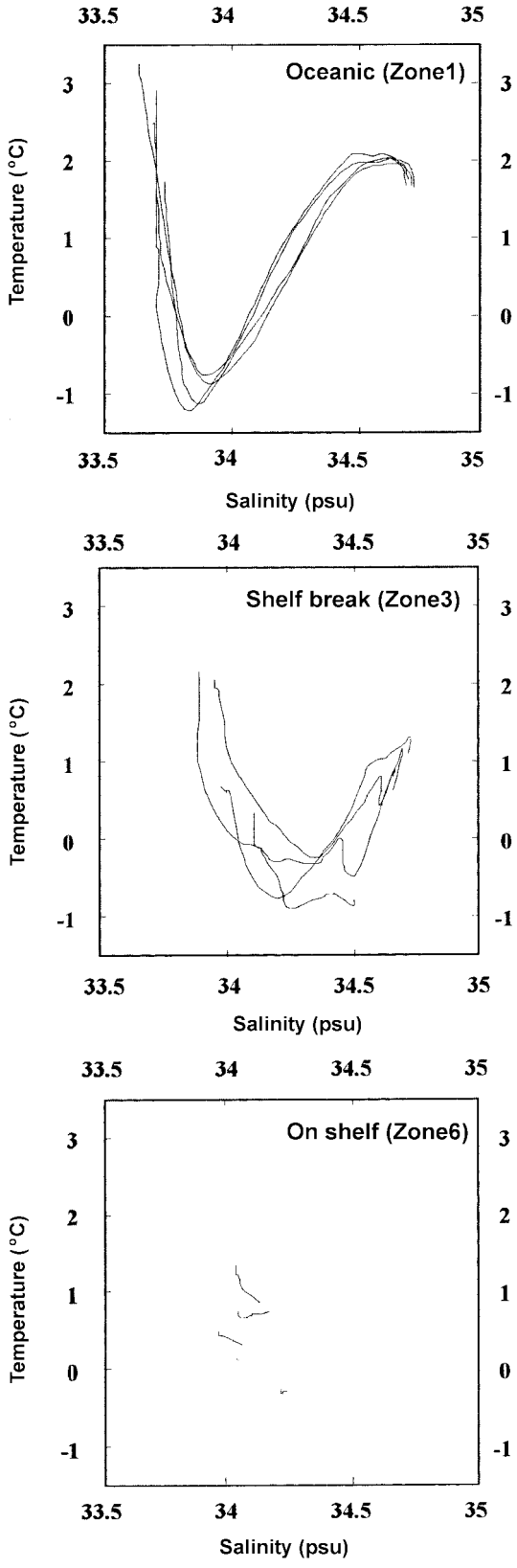

Fig. 2. T/S diagrams characterizing each of the locations where primary productivity experiments were undertaken.

Table 1. Mean ± standard deviation of temperature, salinity, nutrient concentrations, Chl *a* concentration and size composition of chla within the euphotic zone (1 % light depth) within each of the zone (numbers in the brackets indicate the number of data).

Zone	Station	Temp (°C)	Salinity (psu)	SiO_2	NO_2+NO_3	PO_4	Chl *a* (μgl^{-1})	Chl *a* (%)		
				(μM)				pico	nano	micro
Oceanic zone	Stn. A-37, B-59, C-59, D-59	1.78±1.09 (18)	33.686±0.060 (18)	30.5±3.6 (18)	24.9±1.8 (18)	1.77±0.10 (18)	0.16±0.07 (16)	42±11 (16)	30±9 (16)	28±10 (16)
Shelf break zone	Stn. A-41, B-53, C-53, D-53	1.04±1.06 (9)	34.020±0.116 (9)	71.4±2.0 (9)	26.3±1.9 (9)	2.10±0.17 (9)	1.59±0.45 (12)	72±8 (12)	23±9 (12)	5±2 (12)
On shelf zone	Stn. A-50, B-50, C-50, D-50	0.47±0.59 (13)	34.031±0.057 (13)	75.7±1.2 (13)	27.9±1.4 (13)	2.11±0.18 (13)	1.22±0.0.66 (16)	38±27 (16)	26±10 (16)	36±23 (16)

Modified from Shiomoto *et al.* (1998).

and D-50) fell into Zone 6, which do not fit in any of the other zones, and the water columns show little vertical structure.

The physical, chemical and biological parameters within the euphotic zone (1 % light depth) are summarized in Table 1. All of the nutrients, but the silicate at the oceanic stations, seemed to be sufficient (Shiomoto *et al.* 1998). High Chl *a* concentrations were found at the on shelf and shelf break stations, and the concentrations in the oceanic stations were low. The pico-size fraction generally contributed to the total Chl *a* concentrations in all regions.

Table 2. Analysis of deviance for the Chl *a* concentration.

	Df	Deviance	Resid. Df	Resid. Dev	F Value	Pr (F)
NULL			131	22.63		
Zone	2	5.33	129	17.30	26.40	0.000
Size	2	3.22	127	14.08	15.96	<0.000
Temperature	1	0.55	126	13.53	5.40	0.022
Season	3	1.12	123	12.41	3.69	0.014

Statistical analysis for Chl *a* and Chl *a*-specific productivity

The result of the analysis of deviance for Chl *a* concentrations show that zone, size, temperature, and transect are statistically significant factors (Table 2). The mean effect due to a given factor can be illustrated by plotting the predicted value of the dependent variable, and its standard error, for each level of the given factor, with the other factors held fixed. The coefficient for the temperature was +0.0579, which mean that the higher

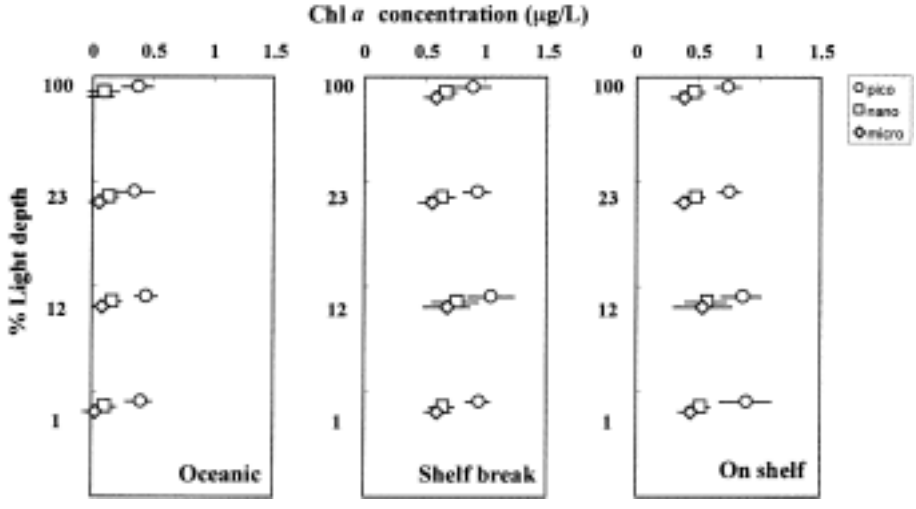

Fig. 3. Predicted Chl *a* concentrations for different station location and depth. The estimates are standardized to the temperature of 0.5 °C. Horizontal solid bars express the standard error.

Table 3. Analysis of deviance for the Chl *a*-specific productivity.

	Df	Deviance	Resid. Df	Resid. Dev	F Value	Pr (F)
NULL			131	295.04		
Depth	3	56.99	128	238.04	12.2947	<0.000
Zone	2	15.21	126	222.83	4.92152	0.009
Mixing Layer	1	6.73	125	216.10	4.3557	0.039
Size	2	26.04	123	190.06	8.42774	<0.000

temperature gives high Chl *a* concentrations. For the prediction, we fixed the temperature to 0.5 °C. Fig. 3 shows the predicted Chl *a* concentrations in each zone. Predicted Chl *a* concentrations both at on shelf and the shelf break stations showed relatively higher values compared to oceanic stations, but showed almost no vertical difference. However, Chl *a* concentrations in pico-size fractions were significantly higher than the nano- and micro-size fractions.

The result of the analysis of deviance for Chl *a*-specific productivity show depth, zone, depth of mixing layer, and size are statistically significant factors (Table 3). The coefficient for the depth of mixing layer was −0.0245, which mean that the deeper mixing layer gives lower Chl *a*-specific production. For the prediction, we fixed the depth of mixing layer to 30 m. Fig. 4 shows the predicted Chl *a*-specific productivity in each zone. Predicted Chl *a*-specific productivity at on shelf stations showed relatively lower values, compared to the oceanic and shelf break station. The productivity decreased with increasing depth, but at all depth, value in pico-size fractions were significantly lower than the nano- and micro-size fractions.

Overview of the environments at the stations for dilution experiments

The temperature and salinity diagrams are shown in Fig. 5. Stns 160, KG, and 224 showed almost no vertical trend. These stations may fall in to zone 6. Stn. 185 exhibited the characteristics of zone 4 water which is slightly cooler and more saline than zone 1-3, with no temperature minimum layer close to 100 m (Holm-Hansen *et al*. 1997). Chl *a* composition only at Stn. KG showed dominancy of micro-size Chl *a*, but the rest of the

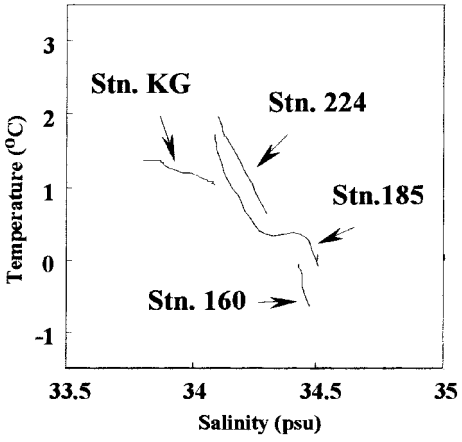

Fig. 5. T/S diagrams characterizing each of the stations where dilution experiments were undertaken.

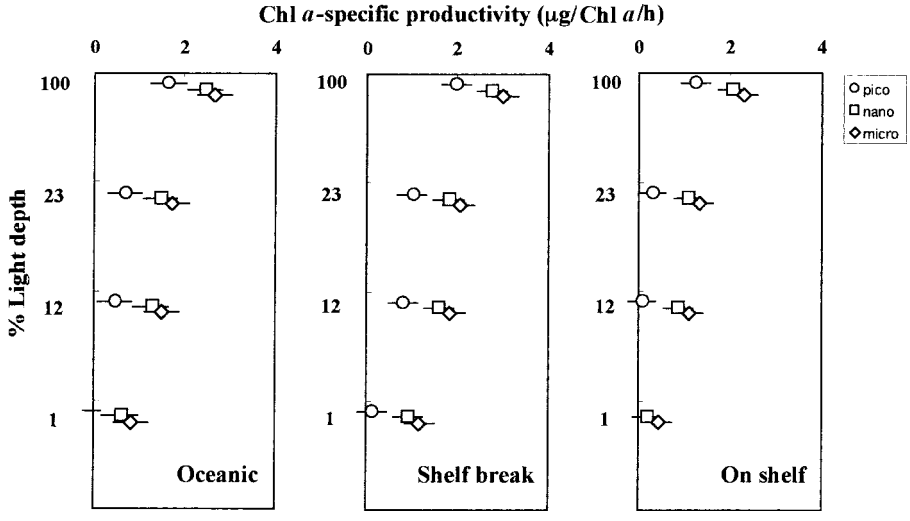

Fig. 4. Predicted Chl *a*-specific productivity for different station location and depth. The estimates are standardized to the depth of mixing layer of 30 m. Horizontal solid bars express the standard error.

Table 4. Phytoplankton growth rates (μ) and microzooplankton grazing rates (g) estimated by the dilution method in the vicinity of the South Shetland Islands during austral summer, 2000.

Stn.	Date	Phytoplankton growth (μday^{-1})			g			Chl *a* (μgl^{-1})			Nutrients (μM)		
		pico	nano	micro	pico	nano	micro	pico	nano	micro	SiO_2	NO_2+NO_3	PO_4
Sta 160	25 Jan. 2000	–0.06	0.15	0.27	0.01	0.13	0.07	0.41(63)*	0.17(25)*	0.08(12)*	69.2	28.5	1.97
Sta 185	30 Jan. 2000	0.13	0.19	0.36	0.11	0.07	0.00	0.57(46)*	0.29(24)*	0.37(30)*	71.1	26.8	1.85
Sta KG	4 Feb. 2000	0.17	0.19	0.39	–0.10	0.05	0.07	0.11(30)*	0.08(22)*	0.18(49)*	72.7	30.3	2.07
Sta 224	6 Feb. 2000	–0.04	–0.03	0.39	0.01	–0.02	–0.06	0.97(62)*	0.36(23)*	0.23(15)*	71.5	30.0	1.95

*Values in the brackets are the percentages to the total Chl *a*.

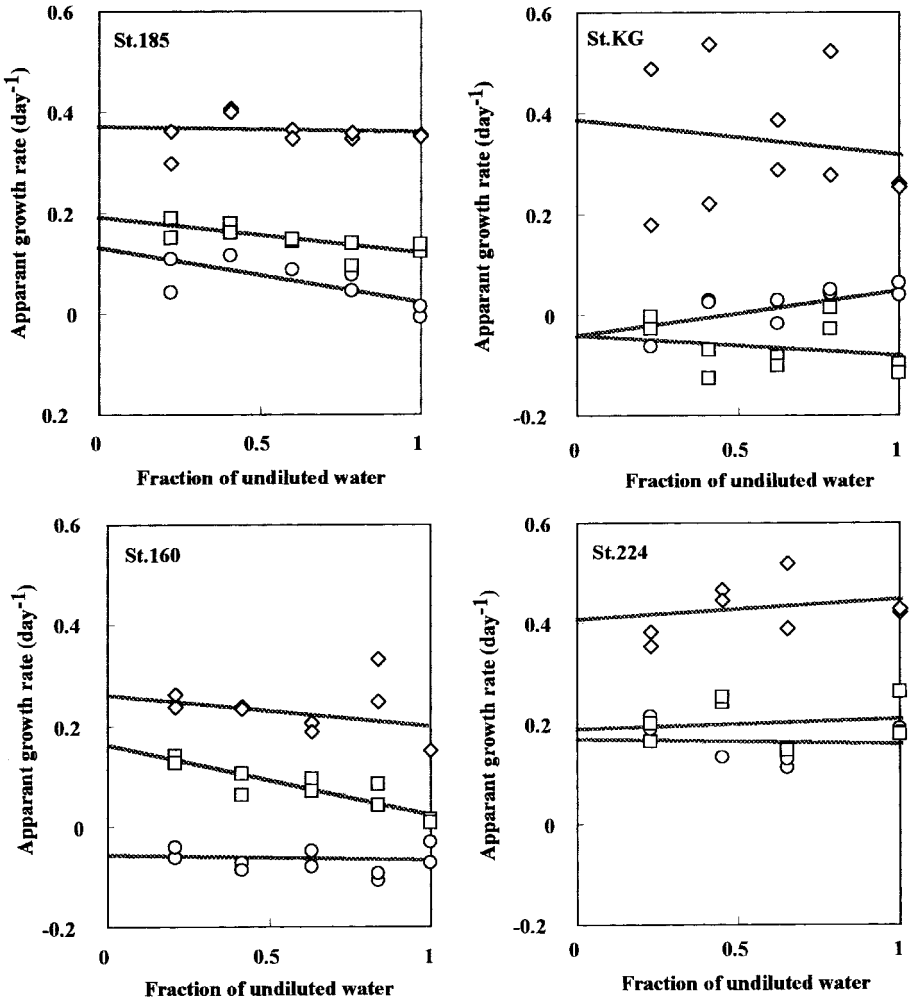

Fig. 6. Relationships between dilution level and apparent growth rate of chlorophyll in pico- nano- and micro-size fractions at each sampling stations.

stations was dominated by pico-size Chl *a* (Table 4).

Phytoplankton growth and microzooplankton grazing measured by diution method

Phytoplankton growth and microzooplankton grazing were variable among the four stations and the size fractions (Table 4, Fig. 6). However, there was a consistent trend, which always showed the highest phytoplankton growth rate in the micro-size fractions. Its statistical significance was confirmed by the analysis of deviance

Table 5. Analysis of deviance for the phytoplankton growth rate measured by the dilution method.

	Df	Deviance	Resid. Df	Resid. Dev	F Value	Pr (F)
NULL			11	0.28		
Size	2	0.20	9	0.09	16.38	0.004
Station	3	0.05	6	0.04	2.77	0.133

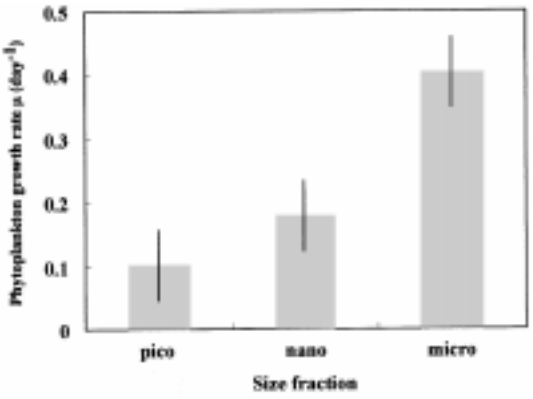

Fig. 7. Predicted phytopalnkton growth rate (μ) in each size fractions. The station was standardized to Stn. 185. The solid vertical bars express the standard error.

Table 6. Result of the non paremetric test (Mann-Whitney U-test) for the comparison between phytoplankton growth rate and microzooplankton grazing.

	Phytoplankton size		
	pico	nano	micro
Pr	0.56	0.24	0.02

using generalized linear model with growth as the dependent variable, and station and size as the categorical factors (Table 5, Fig. 7). Furthermore, the balance between phytoplankton growth and microzooplankton grazing was tested using nonparametric test (Mann-Whitney U-test). Although unbalance between phytoplankton growth and grazing was not observed in both pico- and nano-size fraction, there was significant unbalance in micro-size fraction (Table 6), which revealed higher phytoplankton growth rate compared to the grazing rate.

4. Discussion

Miss match between Chl *a* size composition and their specific production

As shown in this study, although both Chl *a*-specific productivity and growth rate showed significantly high values in larger size fractions (micro-size), the chlorophyll abundance showed significantly high concentrations in smaller size fractions (pico-size). What is the likely explanation for this paradox?

Possibility of the environmental limitations

The analyses of T-S diagrams revealed that the oceanic stations during 1994/95 survey belongs to Zone 1, which might have possibility of causing iron deficiency for phytoplankton growth. Other stations belong to Zone 3 and 6 waters possibly have not been iron limited (Holm-Hansen *et al*. 1997). In our study, although the total Chl *a* concentrations were significantly low in the oceanic region, their Chl *a*-specific productivity was as high as the other stations where irons are thought to be sufficient. This may suggest the negligible effect of iron limitation in our survey.

Thinking of the pre-cleaning procedure and the gear we used (see materials and methods), the possibility of contamination maybe unlikely. Even if the contamination happened, according to previous studies (e.g. Buma *et al*. 1991; Boyd *et al*. 1996), effect of iron may only appear after several days. Our experiments lasted only for 3 hours. Chl *a*-specific productivity was generally higher in the larger size fractions (Fig. 4). If iron deficiency was the major factor, it should have worked advantageous to the productivity in smaller size fractions (Sunda and Huntsman 1997), but didn't. These evidences may suggest that the deficiency of iron may not be the major factor governing the phytoplankton productivity and Chl *a* size composition in our study region.

Size selective removals

Chl *a* abundance in the water is determined through the balance between the production and the removals. Therefore, the miss match in the size fraction between Chl *a*-specific productivity and abundance must be the result of any kinds of removals, and not limitation of growth rate. Selective sinking of larger phytoplanktons are thought to be unlikely, since the vertical profile of the Chl *a* size are generally uniform vertically around this area (Weber and El-Sayed 1987). Another candidate of the removal mechanism maybe the grazing by zooplankton (Cullen 1991).

Possible impact of microzooplankton grazing pressure

Through our dilution experiment, grazing pressure by microzooplanktons in each size fractions was generally

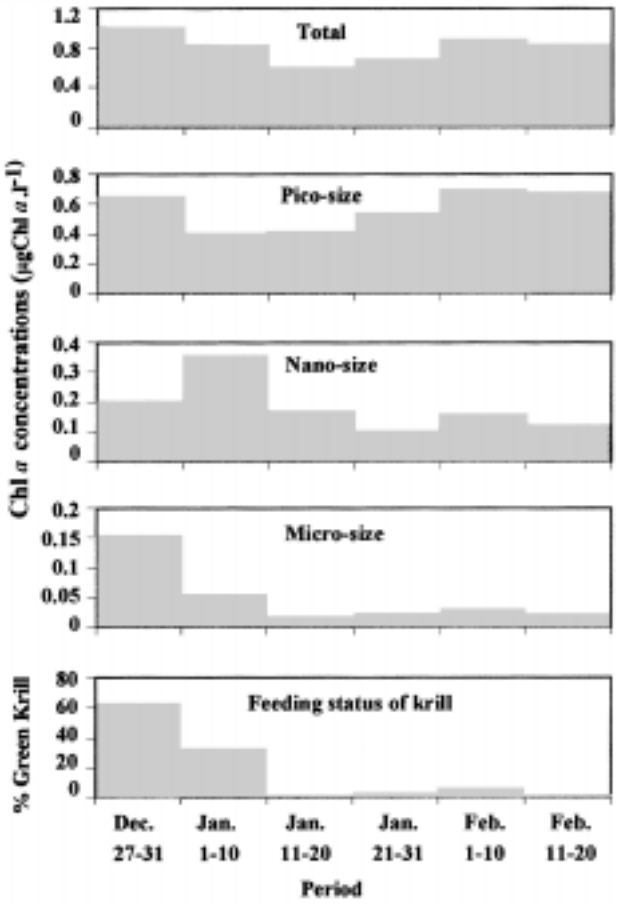

Fig. 8. Chl *a* concentrations in each size fraction, and feeding status of krill in each 10 day period (modified from Kawaguchi *et al.* 1999).

smaller than the phytoplankton growth (Table 4). It seemed that grazing pressure by microzooplankton did not have a major impact on determining the Chl *a* size composition during our observation. Moreover, phytoplankton growth in the micro-size fraction was obviously exceeding the grazing pressure by microzooplankton. On the other hand, Tsuda and Kawaguchi (1997) reported balance between grazing and phytoplankton growth within each size fraction (pico, nano, and micro-size) in the Indian Sector. Hewes *et al*. (1985) pointed out the importance of microzooplankton community in the Southern Ocean. More detailed study is necessary for the further understandings.

Possible impact of krill

Macrozooplanktons such as Antarctic krill, is known as the major consumer of primary production in the Southern Ocean. They are filter feeders whose size selectivity are well documented through laboratory experiments (e.g. Meyer and El-Sayed 1983; Quetine and Ross 1985). Kawaguchi *et al*. (1999), by using the condition of midgut gland as their feeding index, demonstrated that feeding condition of krill is strongly dependent on the availability of micro-size phytoplankton (larger than 10 μm) in the natural environment (Fig. 8). In other words, micro-size phytoplanktons are selectively consumed in the area with high krill density. It maybe worth pointing out that Admiralty Bay in King George Island, where we hardly saw any krill on the echogram, was the only station that showed dominancy of Chl *a* in micro-size fraction (Fig. 9). Changing the scale of our focus, the pattern of circumpolar krill distribution have shown the Antarctic Peninsula as one of the places with very high krill concentration. On the other hand, krill density in the Indian Sector is low (Marr 1962). This characteristics of the Antarctic krill distribution may be one of the explanation to the relatively high share of micro-size Chl *a* compared to share of smaller size Chl *a* in the Indian Sector.

However, this still does not explain the Chl *a* dominance in pico-size fraction in the oceanic area in our study area, since especially in the summer time Antarctic krill mainly distribute on the shelf and the shelf break.

Possible impact of salps

The pelagic tunicate (*Salpa thompsoni*) is also known as an important consumer of the primary production, and their grazing impact may affect the phytoplankton standing stock size (Loeb *et al*. 1997). Although salps are generally categorized as non-selective filter feeders (Madin 1974), their retention efficiency under 2 μm is considerabley low (Kremer and Madin 1992). Onboard experiment suggested that *S. thompsoni* also have lower clearance rate in the smaller size fractions (Kawaguchi *et al.* unpublished data). Since they generally inhabit uniformly low Chl *a* oceanic waters (e.g. Kawaguchi *et al*. 1998; Nicol *et al*. 2000), they may have considerable impact on Chl *a* size composition especially in the oceanic waters where antarctic krill density is low.

5. Conclusion

Through this paper, we presented the miss match of size composition between Chl *a*-specific productivity and their abundance in the waters around the South Shetland Islands. Selective removal by grazing especially by krill and salps, but not limitation of phytoplankton growth,

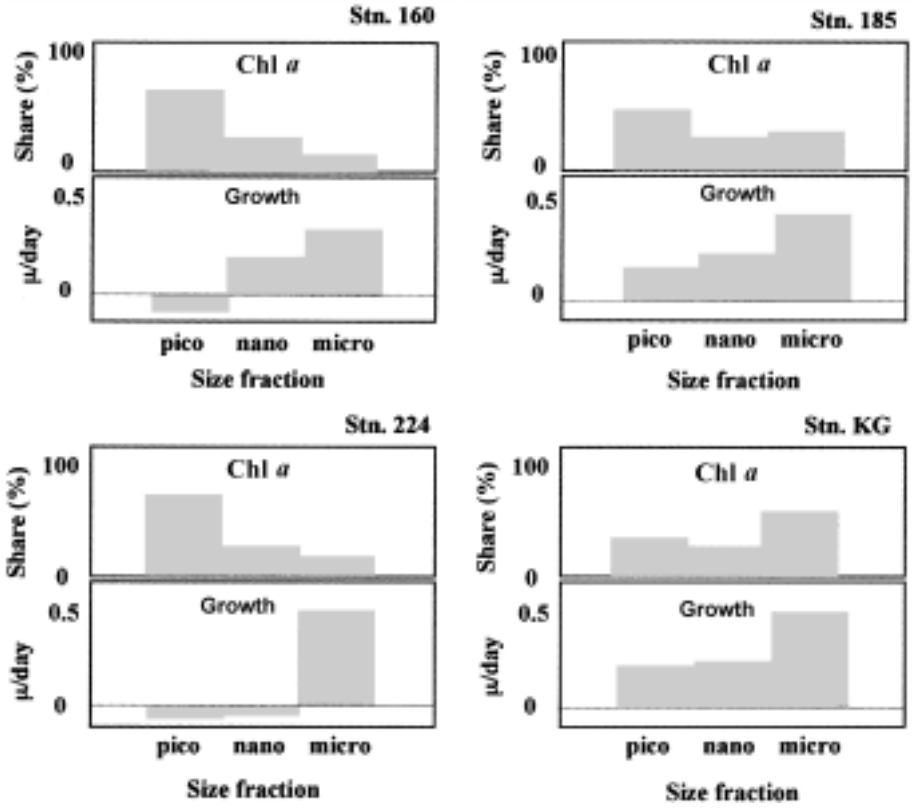

Fig. 9. Share (%) of Chl *a* concentrations and phytoplankton growth in each size fraction measured by dilution method.

seemed to be the major reason. However, the reality is, without doubt far more complex. Quantitative study on zooplankton grazing pressure according to particle size is still desired. At the same time, we could not extend the discussion to the effect of co-limitation of light and iron concentration which Sunda and Huntsuman (1997) suggested. Intensive multi-disciplinary survey in the future will contribute for the better understanding of the paradox.

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