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Nutrient Depletion and Primary Productivity in the Marginal Ice Zone of the Northwestern Weddell Sea During Austral Summer

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Spatial distributions of phytoplankton biomass and nutrients were examined to investigate the magnitude of phytoplankton blooms along the marginal ice zone (MIZ) in the northwestern Weddell Sea during austral summer of 1995. High phytoplankton biomass was associated with the MIZ in the study area. Vertical stability induced by meltwater appears to be the most important factor controlling phytoplankton biomass distribution. Nitrate concentrations are significantly depleted within the upper water column at the phytoplankton biomass maximum. The time required to attain the observed nutrient depletion was calculated from phytoplankton biomass and nitrate depletion, which ranges from 27 to 68 days in transect 4 and from 33 to 145 days in transect 3. Phytoplankton production was also calculated from nitrate depletion and time-scales of nitrate depletion, which varies from 272 to 1752 mg C m^{-2} day^{-1} in transect 4 and from 327 to 2648 mg C m^{-2} day^{-1} in transect 3. In the Southern Ocean where primary productivity shows large temporal and spatial variations, the productivity measurement from nutrient depletion can provide an average rate of primary production during phytoplankton bloom.

INTRODUCTION

The Southern Ocean is a major area of bottom water formation in the World Ocean (Smith, 1990). Surface waters sink and renew deep and intermediate waters of the World Ocean throughout air-sea exchange and sea ice formation. Furthermore, these deep waters derive their physical, chemical, and biological characteristics through processes occurring in the upper waters of the Southern Ocean. A dynamic model to predict the influence of physical and biogeochemical processes on global atmospheric CO_2 concentrations supported the view that the Southern Ocean is essentially neutral with respect to the uptake and release of CO_2 (Tans *et al.*, 1990). However, field measurements of pCO_2 indicated the development of an increased sink for CO_2 in the Southern Ocean (Takahashi, 1993). Recent field measurements at the Bellingshausen Sea found strong CO_2 uptake, which is consistent with biological uptake (Robertson and Watson, 1995; Turner and Owens, 1995). As the current circulation is characterized by divergence and convergence in the Southern Ocean, the patterns of CO_2 uptake and release is very complex. The difficulty in predicting CO_2 uptake and release is also derived from the paucity of relevant physical, chemical, and biological observations from the Southern Ocean.

Despite high concentrations of macronutrients in surface waters throughout the year, phytoplankton biomass and primary production are low in offshore regions of the Southern Ocean (Holm-Hansen *et al.*, 1977; El-Sayed, 1988). Thus, the Southern Ocean has been described as a High Nutrient, Low Chlorophyll (HNLC) region. However, field works and satellite ocean color images have revealed high primary productivity in areas with salinity-induced stability associated with the marginal ice zone (MIZ) or in coastal and continental shelf areas (Sullivan *et al.*, 1988; Comiso *et al.*, 1990; Mitchell and Holm-Hansen, 1991; Laubscher *et al.*, 1993). High phytoplankton biomass is also associated with an oceanic frontal zone in the Bellingshausen Sea (Boyd *et al.*, 1995). Smetacek *et al.* (1997) confirmed the suggestion that frontal regions are the major productive sites in the Southern Ocean. Therefore, there is a need for more observations on the mechanisms controlling magnitude of phytoplankton blooms in the Southern Ocean.

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The nutrient uptake has been well correlated with primary production in a variety of pelagic ecosystem (Whitehouse *et al.*, 1995; Priddle *et al.*, 1998). Jennings *et al.* (1984) calculated primary production from nutrient depletion in the upper water column and observed that nutrient depletion represented much higher primary productivity than isotopic productivity measurements. They suggested that the productivity measurement from nutrient depletion inherently includes the contribution of phytoplankton bloom during austral spring, but it may be missed by the isotopic productivity measurement. The relatively sparse data set of isotopic productivity measurements cannot provide detail information on phytoplankton blooms in the Southern Ocean where primary productivity shows a large spatial and temporal variation (Wiggert *et al.*, 1994). In this paper, it is described the vertical and horizontal distributions of nutrients and phytoplankton biomass along the MIZ in the northwestern Weddell Sea during the austral summer. Primary productivities are calculated from nitrate depletions in the upper water column and compared with isotopic productivity measurements.

MATERIALS AND METHODS

Nutrient and chlorophyll *a* were measured aboard the R/V *Yuzhmorgeologiya* during early January 1995 in the northwestern Weddell Sea (Fig. 1). Vertical nutrient and chlorophyll *a* profiles were observed at 19 stations along two north-south transects perpendicular to the ice-edge. Most stations along transect

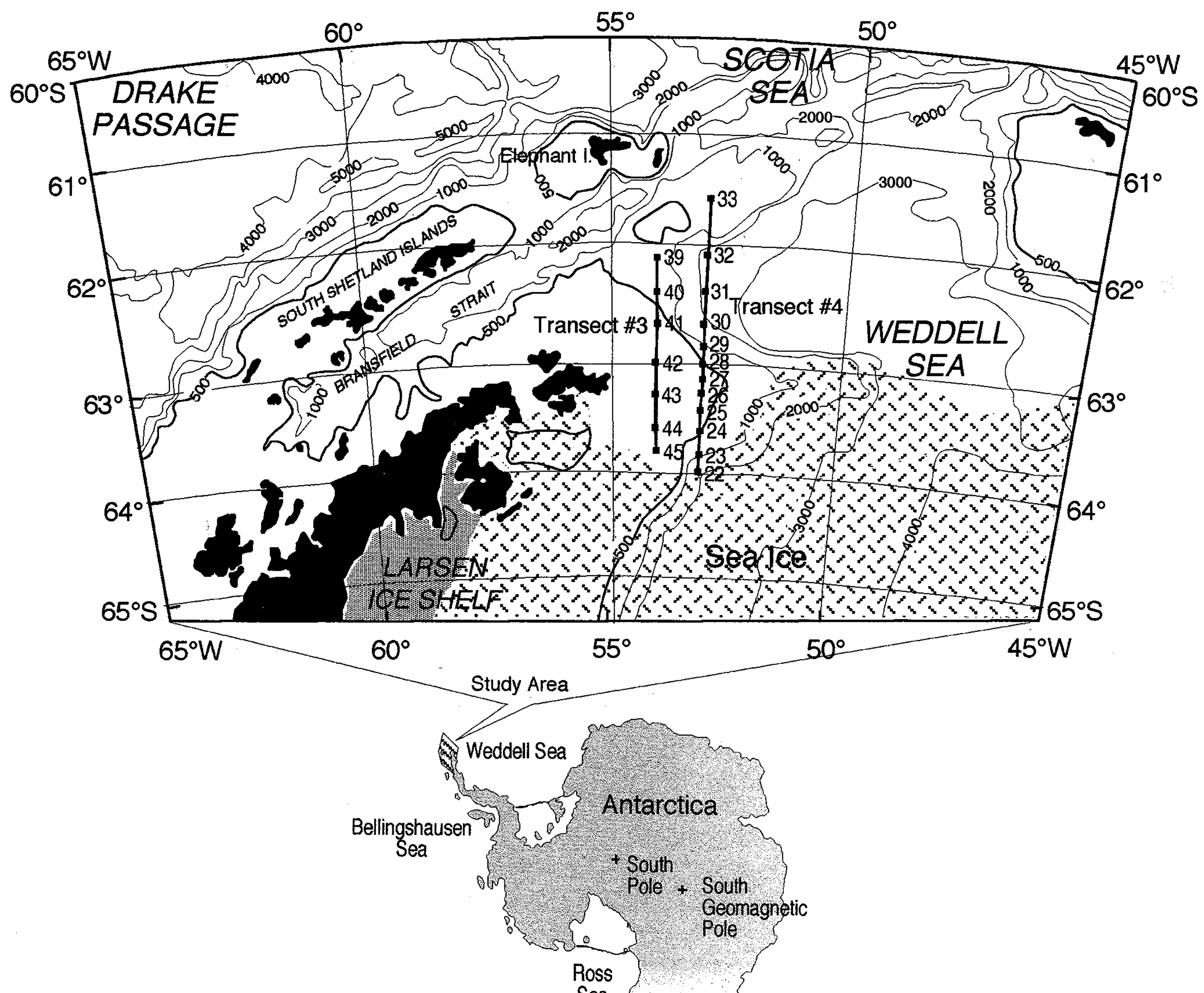

Fig. 1. Study area and sampling stations along transects 3 and 4.

4 were located in the deep waters (deeper than 500 m), whereas five out of seven stations along transect 3 were in continental shelf waters (shallower than 500 m). These transects were 200–300 km long, and samples were taken within three days; January 9th to 11th for transect 4 and January 13th to 14th for transect 3. Water temperature and salinity were measured with a Neil-Brown CTD mounted on a Rosette sampler.

Water samples for nutrient and chlorophyll *a* measurements were collected with 5 liter Niskin water sampler at 8 water depths (0, 10, 20, 30, 50, 75, 100, 150 m). For the measurement of nutrients (nitrate, phosphate, silicate), about 500 ml of seawater samples were filtered through Whatman GF/F filters, and the filterates were frozen at 20°C in acid-cleaned polyethylene bottles. Nutrient concentrations were determined with a SKALAR 5100 auto-analyzer following the methods of Parsons *et al.* (1984). Chlorophyll *a* concentrations were determined by a spectrophotometric method after filteration on Whatman GF/F filters and extraction in 90% acetone (Parsons *et al.*, 1984).

RESULTS

In transect 4, the vertical distribution of temperature displayed that a tongue of cold water extends northward at a depth of about 60–140 m (Fig. 2a). This cold core represents Weddell Sea Winter Water, a remnant from the proceeding winters cold convective layer (Carmack, 1977). The upper water column was well stratified in salinity and seawater density in transect 4, except for stations 32 and 33 (Figs. 2b and 2c). The upper mixed layer was 20–60 m deep at all stations. Vertical profiles of salinity showed two cores, centered at stations 25 and 29 where surface salinity displayed the lowest value. Surface salinity varied from 33.76 to 34.33 psu, with the lowest value at station 25 and the highest value at station 33. Salinity and seawater density increased gradually with increasing water depth. The vertical distribution of salinity was quite similar to that of seawater density, implying that salinity was the main factor determining seawater density in this transect.

Chlorophyll *a* showed maximum concentrations near the ice edge in transect 4, located at stations 22–26 (Fig. 2d). The highest chlorophyll *a* concentration exceeded 12 $\mu g\ l^{-1}$, which was observed at a 30 m water depth of station 23. Phytoplankton biomass maxima occurred at the low-salinity surface water derived from ice melt. The phytoplankton biomass maximum was associated with nitrate concentration minima (Fig. 2e). Surface nitrate concentrations ranged from 7.4 to 28.4 μM with the lowest value at station 25 and the highest value at station 33. Surface nitrate depletion was not observed at stations 32 and 33 where chlorophyll *a* concentrations were relatively low. Vertical distribution of silicic acid concentrations was significantly different from that of nitrate concentrations (Fig. 2f). Silicic acid concentrations were relatively low near the phytoplankton biomass maximum. High silicic acid concentrations were observed at a depth of 40–120 m at station 33.

The cold water core was also found at a depth of 60–120 m in transect 3. However, it was less extended northward compared with transect 4. Salinity and seawater density were well stratified within the upper water column near the ice edge and the north side of the transect (Figs 3b and 3c). Stations 42 was well mixed within the upper 140 m. Surface salinity was between 33.95 and 34.38 psu, with the lowest value at station 45 and the highest value at station 42. Surface salinity and density near the ice edge zone were generally higher in transect 3 than in transect 4. Salinity showed a similar vertical distribution with seawater density in this transect, implying that seawater density was mainly controlled by salinity.

Chlorophyll *a* exhibited maximum concentrations (~13.3 $\mu g\ l^{-1}$) near the ice edge, but not at the northern stations of transect 3 where the upper water column was stratified in salinity and seawater density (Fig. 3d). Phytoplankton biomass maxima were also observed at the low-salinity surface water in this transect. The most distinct feature in the vertical distribution of chlorophyll *a* was that the chlorophyll *a* maximum extended into deeper waters down to 140 m. Park *et al.* (1999) suggested that the deep high phytoplankton biomass resulted from passive sinking of phytoplankton population dominated by *Phaeocystis antarctica* from the surface waters. Surface nitrate concentrations varied from 7.5 to 26.8 mM, with the lowest value at station 45 and the highest value at station 39. Nitrate concentration minima were associated with the phytoplankton biomass maxima (Fig. 3e). However, nitrate depletion occurred only in the upper water column, even though the phytoplankton biomass maximun extended into deeper waters. The surface nitrate depletion was also observed at stations 40 and 41 where chlorophyll *a* concentrations were low and the mixed layer is relatively

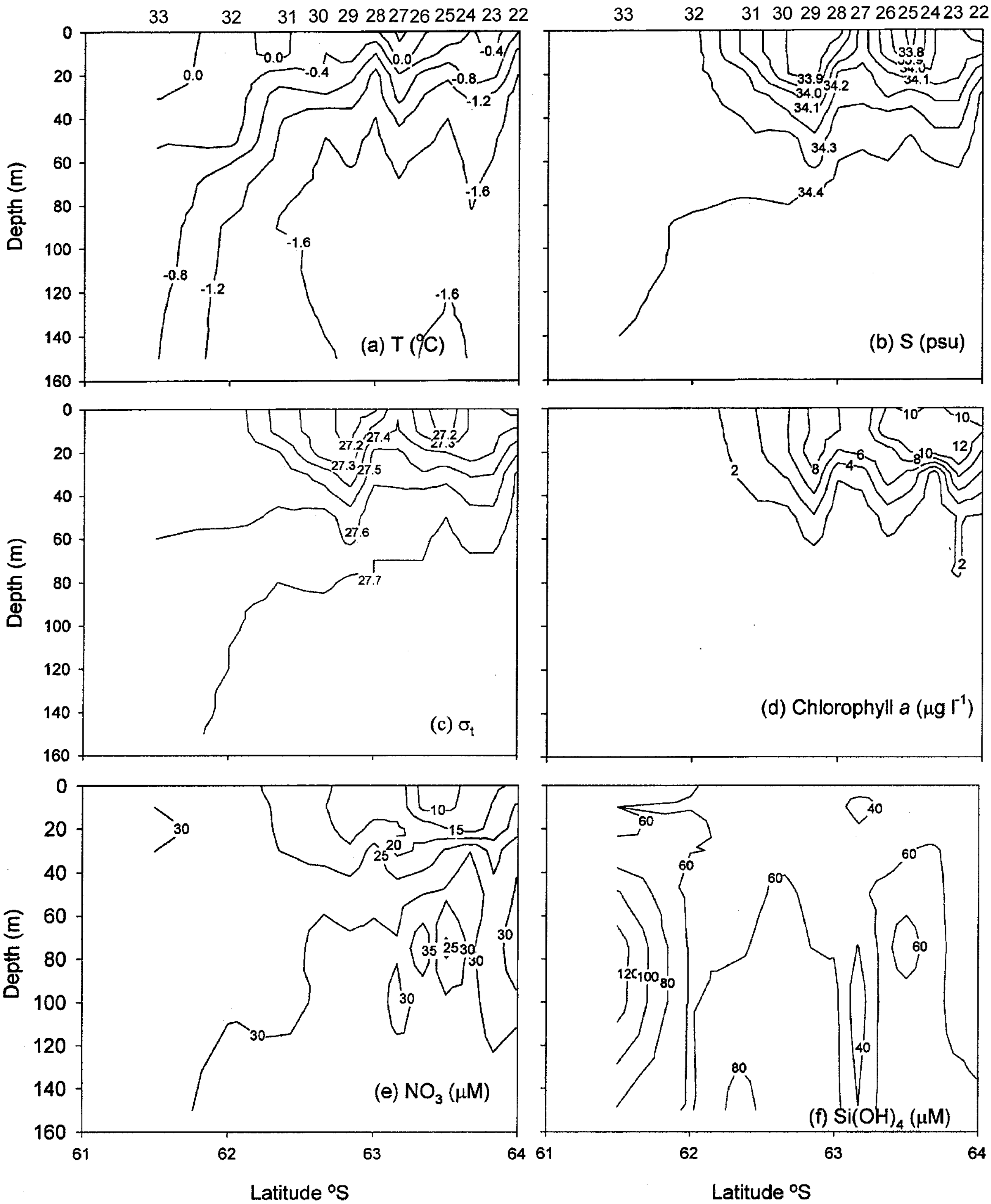

Fig. 2. Vertical sections of (a) temperature, (b) salinity, (c) seawater density, (d) chlorophyll *a*, (e) nitrate, and (f) silicic acid along transect 4.

deep. Silicic acid concentration minima were also associated with the phytoplankton biomass maxima (Fig. 3f). Silicic acid exhibited high concentrations at a 100–140 m of stations 39 and 40.

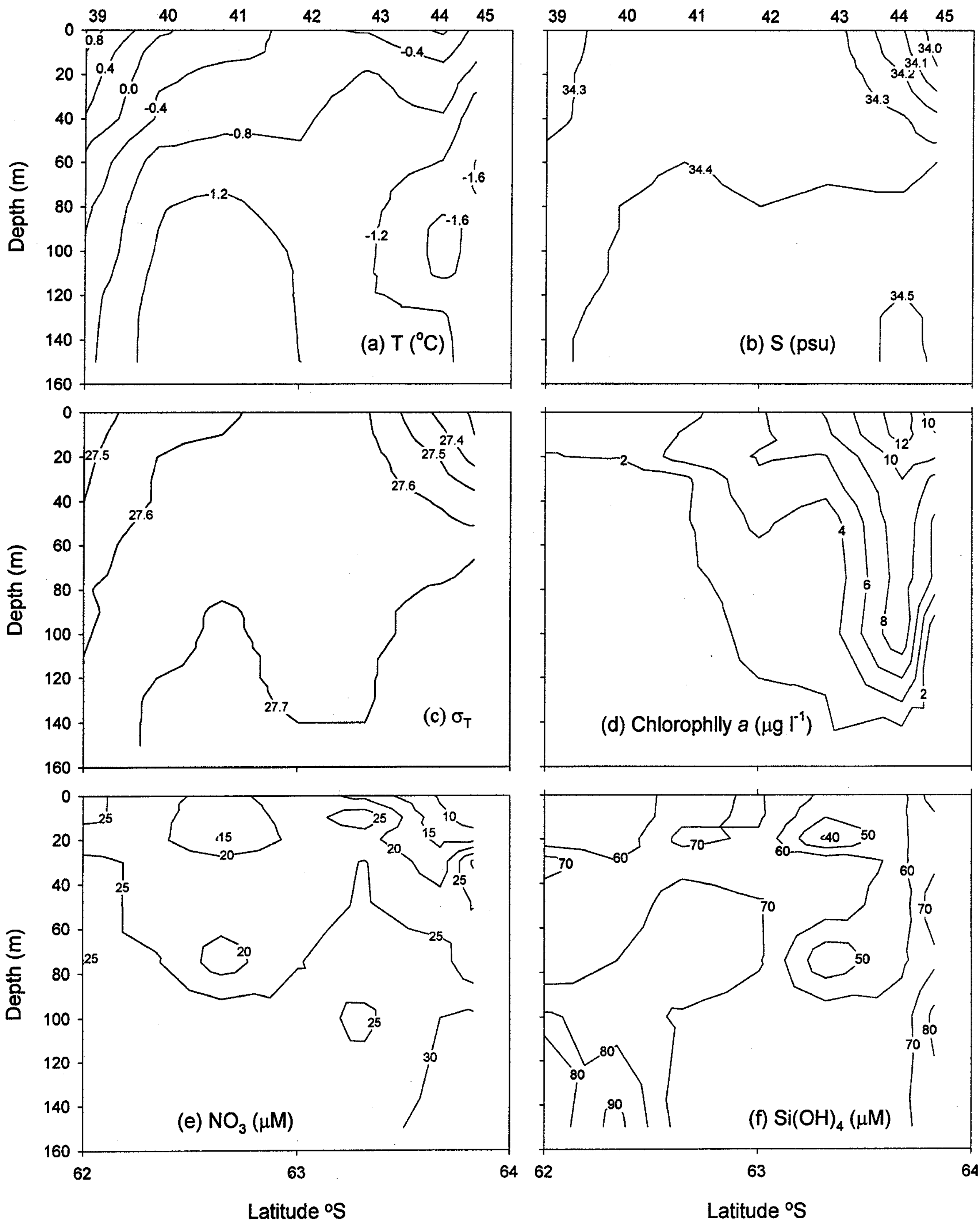

Fig. 3. Vertical sections of (a) temperature, (b) salinity, (c) seawater density, (d) chlorophyll *a*, (e) nitrate, and (f) silicic acid along transect 3.

DISCUSSION

Phytoplankton biomass shows high values at the MIZ in both transect, which has previously been observed in high-latitude areas (Smith *et al.*, 1985; Nelson and Smith, 1986; Nelson *et al.*, 1987; Smith and Garrison, 1990). Vertical stability induced by melt-water is likely the most important factor controlling

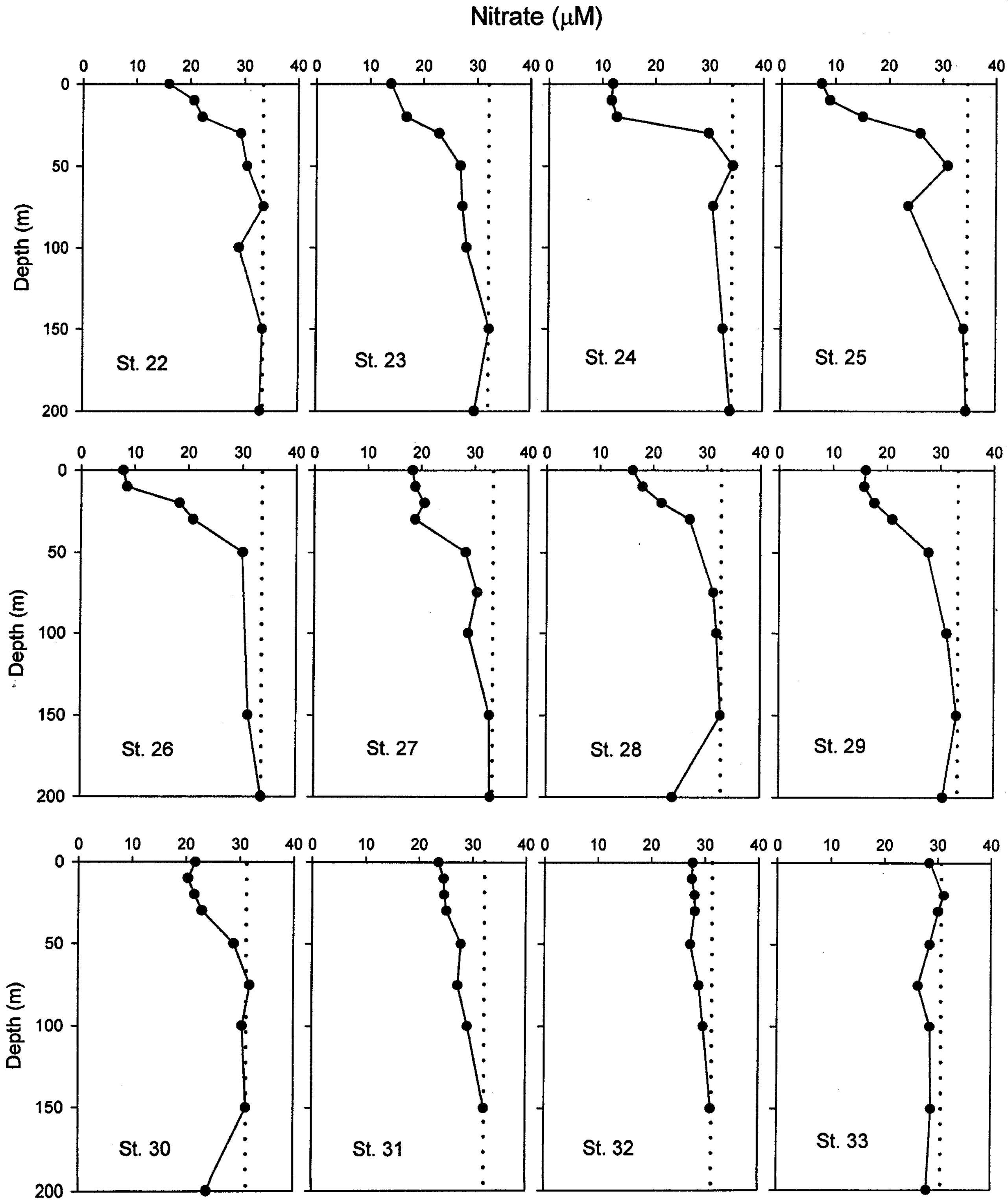

Fig. 4. Vertical profiles of nitrate concentrations (μM) in transect 4. Dotted line represents the winter nitrate concentration that is determined as a nitrate concentration below 100 m depth.

phytoplankton biomass distribution in this study area. Nitrate concentrations are significantly depleted within the upper water column at the phytoplankton biomass maximum, implying that nitrate concentration is strongly affected by *in situ* uptake by phytoplankton (Smith *et al.*, 1985; Nelson *et al.*, 1987). Nutrient depletions within the upper water column can provide information on phytoplankton production if the timescale of nutrient depletion is defined (Jennings *et al.*, 1984; Karl *et al.*, 1991; Whitehouse *et al.*, 1995). Vertical profiles of nitrate in transects 4 and 3 are shown in Figures 4 and 5 in which dotted lines represent the winter nitrate concentration that is determined as a nitrate concentration below 100 m depth. Nitrate depletions were estimated as depth integration of differences between the observed and winter nitrate concentrations. Nitrate depletion was not estimated at station 33 due to constant nitrate concentrations throughout the water column (Fig. 4). Nitrate depletions range from 273 to 1088 mmol m^{-2} in transect 4 and from 463 to 1330 mmol m^{-2} in transect 3 (Table 1). Nitrate depletion is generally larger when phytoplankton biomass is high. Our estimates of nitrate depletion are almost twice as much as other estimates in the Weddell Sea and slightly higher than that in the Ross Sea (Table 2). Vertical distributions of chlorophyll *a* are displayed in Figs. 6 and 7 in both transects. Depth-integrated chlorophyll biomass is listed in Table 1. Nitrate depletion is well correlated with the depth-integrated chlorophyll biomass (R^2=0.55, $p<0.001$).

In order to calculate primary productivity from

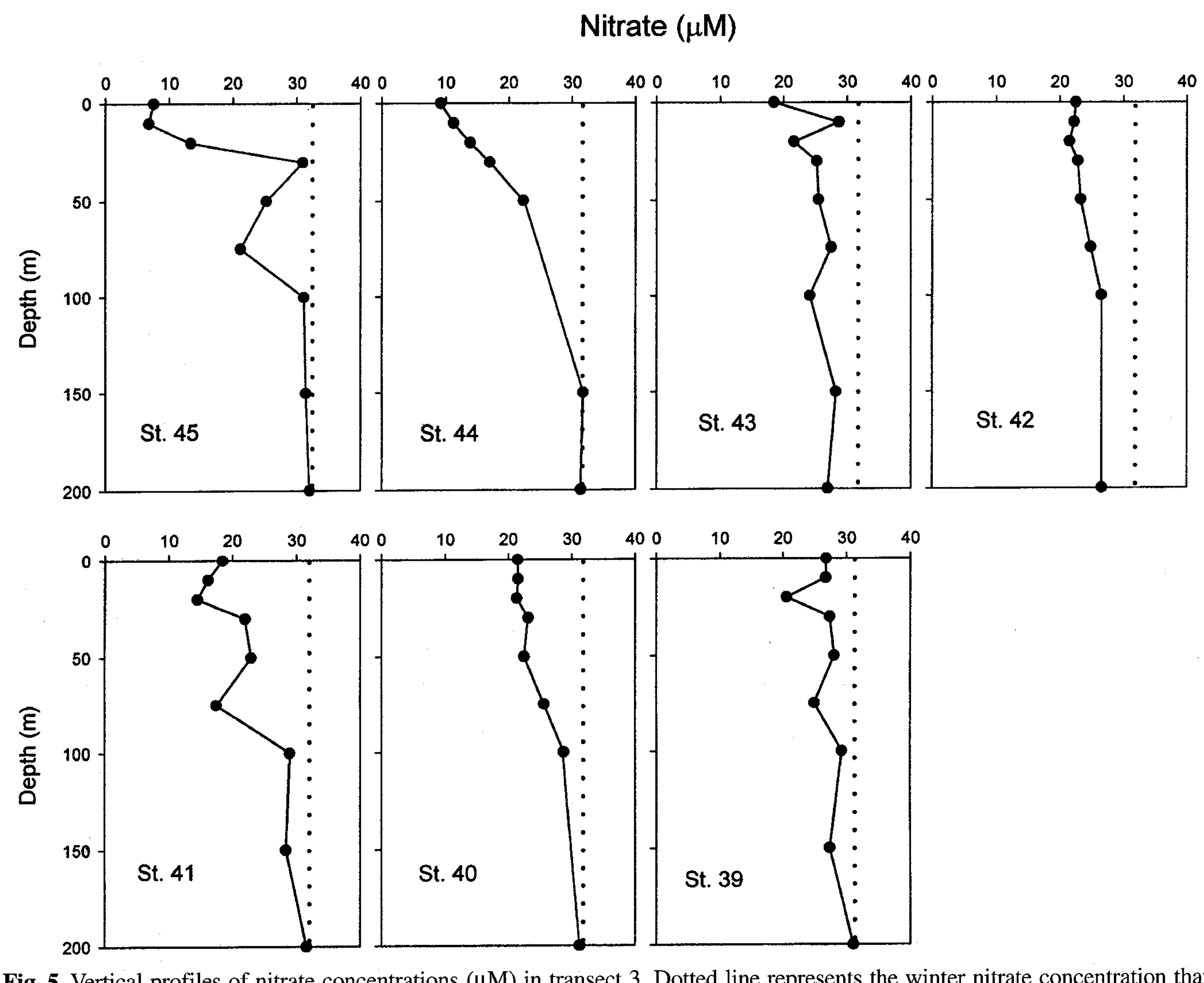

Fig. 5. Vertical profiles of nitrate concentrations (μM) in transect 3. Dotted line represents the winter nitrate concentration that is determined as a nitrate concentration below 100 m depth. At stations 43 and 42, winter nitrate concentrations were determined as an average nitrate concentration below 100 m at other stations of transect 3 because nitrate concentrations below 100 m at these stations were fairly low compared with those at other stations.

Table 1. Primary production calculated from nitrate depletions

Stations	Integrated nitrate depletion (mmol m^{-2})	Integrated chlorophyll (mg m^{-2})	Time scales of nitrate depletion (days)	Primary productivity (mg C m^{-2} d^{-1})	Annual productivity (g C m^{-2} yr^{-1})
22	493	383	27	1236	33.3
23	828	517	32	1751	56.0
24	688	340	40	1164	46.5
25	1088	416	52	1416	73.6
26	800	438	36	1504	54.1
27	758	239	63	814	51.3
28	593	245	48	836	40.1
29	810	444	36	1523	54.8
30	473	256	37	865	40.0
31	538	163	66	552	36.4
32	273	80	68	272	18.5
45	1020	625	33	2092	69.0
44	1330	788	34	2648	90.0
43	1020	529	38	1817	69.0
42	1075	533	40	1819	72.7
41	1135	215	105	732	76.8
40	700	96	145	327	47.3
39	463	170	54	580	31.3

Table 2. Summary of average nitrate depletions from previous studies in the Southern Ocean

Locations	Season	Nitrate depletion (mmol m^{-2})	References
Weddell Sea	summer	300	Jennings *et al.* (1984)
Ross Sea	summer	600	Nelson and Smith (1986)
Weddell-Scotia confluence	spring	350	Nelson *et al.* (1987)
Western Weddell Sea	spring	275	Bianchi *et al.* (1992)
Bellingshausen Sea	spring	273	Whitehouse *et al.* (1995)
Northwestern Weddell Sea	summer	783	This study

nitrate depletion, it is assumed that vertical mixing does not take place to change nitrate concentrations within the euphotic zone. Seawater density is well stratified within the upper water column at most stations of both transects (Figs 2 and 3). Thus, vertical mixing does unlikely alter nitrate concentrations significantly within the euphotic zone. It is also required the carbon: nitrogen ratio of phytoplankton and the time required to attain the observed nitrate depletion. Jennings *et al.* (1984) calculated an annual primary production from nutrient depletions by using a C:N:P =62:11:1 which is more representative for Antarctic phytoplankton than the Redfield ratio (Copin-Montegut and Copin-Montegut, 1978). Whitehouse *et al.* (1995) estimated the time required to attain the observed nutrient depletion, assuming that phytoplankton biomass has not changed during nitrate depletion, and a growth rate is 0.1 day^{-1} (Boyd *et al.*, 1995). In order to convert chlorophyll biomass to nitrate uptake, we used a carbon:chlorophyll weight ratio of 34 measured at open water stations in the Bellingshausen Sea (Robins *et al.*, 1995). The time required for nitrate depletion is calculated by the following equation;

$$\text{Time (day)}=\frac{\text{nitrate depletion}\times\text{C:N ratio}\times\text{carbon molar weight}}{\text{chlorophyll } a\times\text{carbon:chlorophyll ratio}\times\text{growth rate}}$$

Here, chlorophyll a indicates depth-integrated chlorophyll *a* (mg m^{-2}), and growth rate represents a phytoplankton growth rate (0.1 day^{-1}). The time scales of nitrate depletion do not show a large spatial variation in transect 4, with a range of 27–68 days (Table 1). On the other hand, they vary by five times of magnitudes in transect 3, with a maximum day (145 day) at station 40. These time scales are rather comparable with those (64–87 days) estimated in the

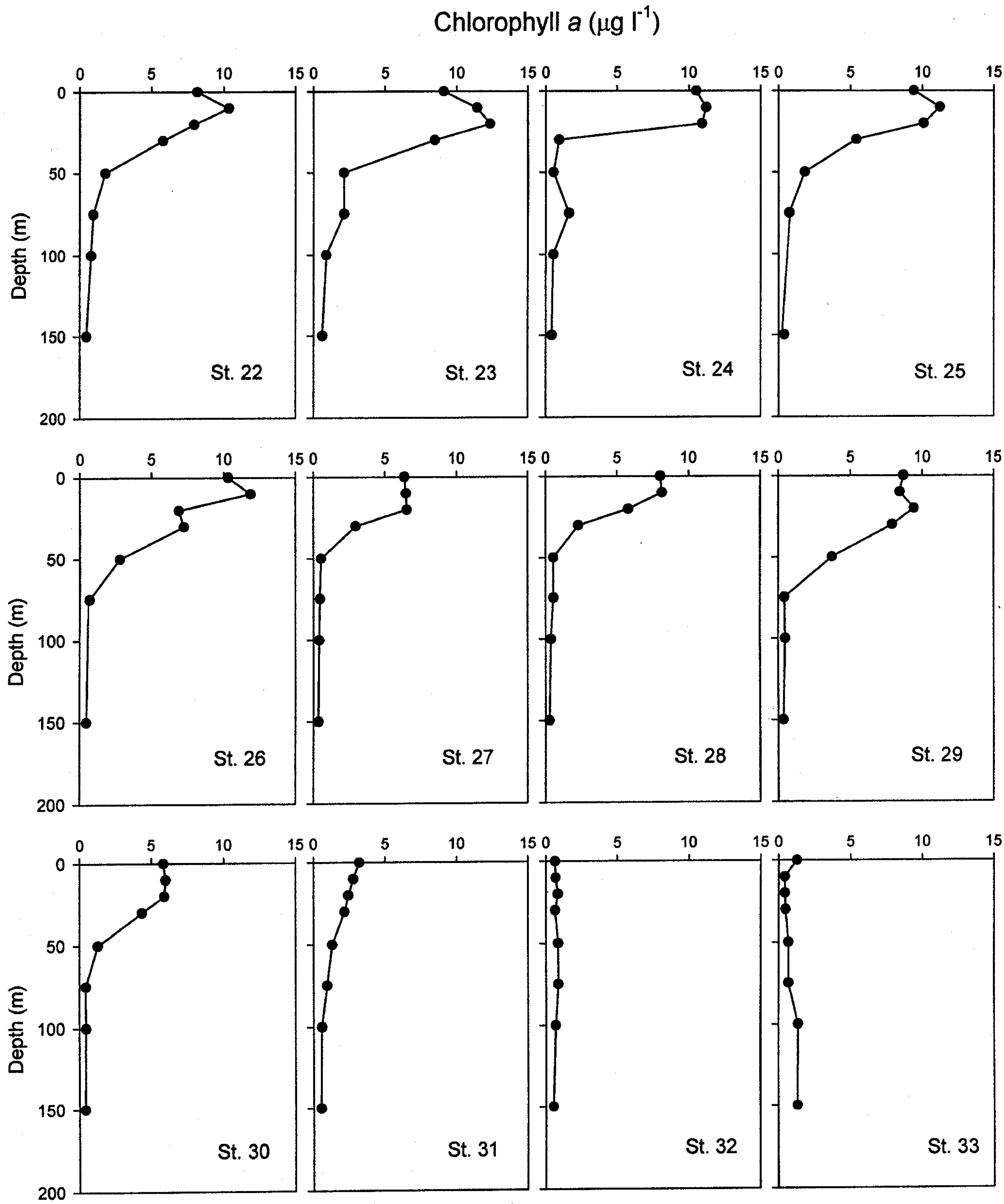

Fig. 6. Vertical profiles of chlorophyll *a* concentrations (μg l^{-1}) in transect 4.

Bellingshausen Sea (Whitehouse *et al.*, 1995). Jennings *et al.* (1984) calculated primary productivity from nutrient depletions based on the average rates of depletion over the 60 and 90 day time frame. Phytoplankton bloom has sustained for more than 2 months in coastal regions of the Antarctic Peninsula (Holm-

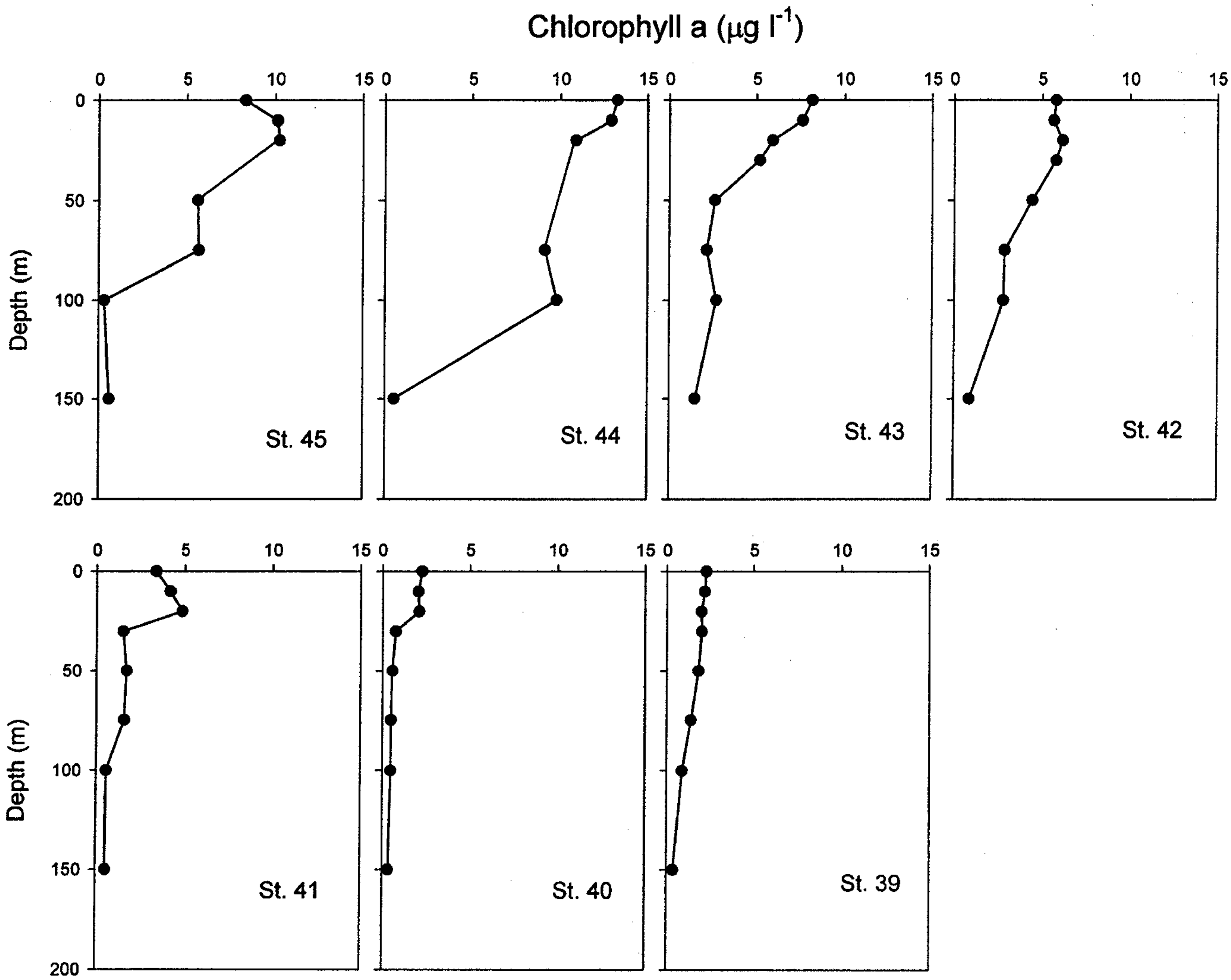

Fig. 7. Vertical profiles of chlorophyll *a* concentrations (μg l^{-1}) in transect 3.

Hansen and Mitchell, 1991). Phytoplankton bloom has persisted for 27–40 days near the MIZ in this study area. The time scales of nitrate depletion are relatively short near the MIZ and increase away from the MIZ.

Primary production was calculated from nitrate depletion and the time required for nitrate depletion (Table 1). They range from 272 to 1752 mg C m^{-2} day^{-1} in transect 4 and from 327 to 2648 mg C m^{-2} day^{-1} in transect 3. The calculated primary production near the MIZ is somewhat higher in transect 3 than in transect 4. They are plotted against the direct isotopic productivity measurements at the same stations in Fig. 8. The data of isotopic productivity measurements come from Park *et al.* (1999). The calculated productivity from nitrate depletions is somewhat lower at most stations than the productivity measured by the isotopic incubation method. The isotopic productivity measurement was conducted during early January when primary productivity is usually the highest rate in the year in the Southern Ocean (Holm-Hansen and Mitchell, 1991). The isotopic measurement is fairly dependent on weather conditions during incubation and thereby, the measured productivity is rather variable, even in similar environmental conditions. Park *et al.* (1999) reported a large spatial variation in their productivity measurements. Thus, the isotopic productivity measurement is unlike to provide the actual primary production during phytoplankton bloom. However, the calculated productivity from nitrate depletions indicates an average rate during phytoplankton bloom.

Annual primary productions in the study area were calculated for nitrate depletions, which range from 18.5 to 73.6 g C m^{-2} yr^{-1} in transect 4 and from 31.3 to 90.0 g C m^{-2} yr^{-1} in transect 3 (Table 1). At the

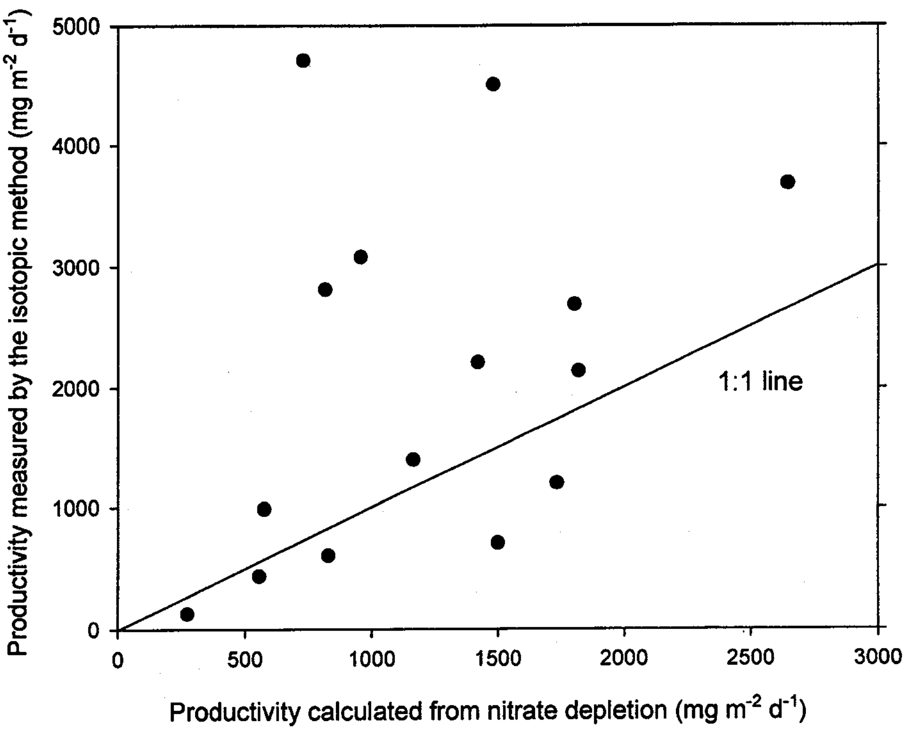

Fig. 8. The plot of productivity calculated from nitrate depletions versus productivity measured by isotopic incubation method. Solid line indicates 1:1 line.

MIZ of both transects, annual production vary from 33.3 to 90.0 g C m^{-2} yr^{-1}, with an average of 54.9 g C m^{-2} yr^{-1}, which is much lower than that (132 g C m^{-2} yr^{-1}) estimated on the basis of phytoplankton pigment concentrations from the coastal zone color scannar at the MIZ of the Weddell Sea (Arrigo *et al.*, 1998). The productivity measurement from nitrate depletion represents a minimum rate because of internal recycling of nitrate within the euphotic zone (Jennings *et al.*, 1984). Some organic nitrogen is remineralized by microbial activity within the euphotic zone and thereby, ammonium, the by-product of remineralization enters into the euphotic zone. Phytoplankton preferentially takes up ammonium to nitrate. Thus, the productivity calculated from nitrate depletion might be underestimated. About half of total primary production is supported by nitrate during ice-edge phytoplankton bloom in the Weddell and Ross Sea (Nelson and Smith, 1986; Smith and Nelson, 1990). If we consider the primary production supported by ammonium, the average annual production at the MIZ of both transects is 110 g C m^{-2} yr^{-1}, which is rather similar to that estimated by Arrigo *et al.* (1998).

The productivity measurement form nutrient depletion has its own problems, such as the internal recycling of nutrient and vertical mixing. However, it gives valuable information on an annual primary production and the average productivity during phytoplankton bloom which are hardly estimated by the isotopic productivity measurement. In the Southern Ocean, therefore, the productivity estimation from nutrient depletion can provide an average rate of the highly variable primary production.

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