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Interannual variations in nutrients, net community production, and biogeochemical cycles in the Ross Sea

Walker O. Smith Jr.[a,*], Amy R. Shields[a], Jill A. Peloquin[a], Giulio Catalano[b], Sasha Tozzi[a], Michael S. Dinniman[c], Vernon A. Asper[d]

[a]*Virginia Institute of Marine Sciences, College of William and Mary, Gloucester Pt., VA 23062, USA*
[b]*CNR-Institute for Marine Sciences, Viale Gessi, 2, 34123 Trieste, Italy*
[c]*Center for Coastal Physical Oceanography, Old Dominion University, Norfolk, VA 23529, USA*
[d]*Department of Marine Science, University of Southern Mississippi, Stennis Space Center, MS 39529, USA*

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Abstract

The Ross Sea continental shelf is dominated by the seasonal appearance of a large phytoplankton bloom. This bloom is regularly dominated by diatoms and the haptophyte *Phaeocystis antarctica*, and significant nutrient (nitrogen and silicon) reductions within the water column occur during the growing season (early November to late February). Diatoms mediate silicic acid removal, whereas both taxa remove nitrate. Dissolved and particulate nitrogen and silica concentrations were collected from a series of cruises to the southern Ross Sea over 3 years. Simple, one-dimensional nutrient budgets were generated for nitrogen and silica, and estimates of vertical flux were derived from these budgets. Substantial variations among years are observed to occur in seasonal community production, assemblage composition, Si:N uptake ratios, and export, and standard deviations are equal to ~30% of the mean. During 2003–2004 a large *Phaeocystis antarctica* bloom occurred in December, and was followed by a bloom of diatoms. This secondary bloom was equal in magnitude to that of the initial *P. antarctica* bloom. In contrast, no secondary bloom was observed in 2001–2002. Continuous fluorescence measurements suggested that the spatial–temporal mosaic of phytoplankton dynamics in the Ross Sea is far more complex than previously thought. We hypothesize that variations occur between years not only in terms of both magnitude and composition of the bloom, but also in the controlling mechanisms.

Keywords: Ross Sea; Nutrients; *Phaeocystis*; Fluorescence; Nitrogen; Silica; Production

1. Introduction

During the past 15 years the biogeochemistry of the Ross Sea has been intensively investigated by several large programs (e.g., Smith and Anderson, 2003), and the details of the carbon, nitrogen and silica budgets are as well known as any location in the Antarctic (Nelson et al., 1996; Sweeney et al., 2000a; Arrigo et al., 2002). In addition, satellite observations have provided both continuous observations on ice distribution and concentration, as well as estimates of phytoplankton pigment concentrations (Comiso et al., 1993; Arrigo and McLain, 1994; Arrigo et al., 2003). Direct estimates

*Corresponding author. Tel.: +1 804 684 7709; fax: +1 804 684 7399.
E-mail address: wos@vims.edu (W.O. Smith Jr.).

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of primary production (Smith and Gordon, 1997; Saggiomo et al., 1998) and of vertical fluxes of biogenic material (Dunbar et al., 1998; Asper and Smith, 1999; Collier et al., 2000; Accornero and Gowing, 2003) also have been made. These biomass and production measurements have demonstrated that the Ross Sea as a whole is the most productive region in the entire Southern Ocean. Annual productivity estimates exceed $200\,g\,C\,m^{-2}$, and while not exceptionally great relative to the entire ocean, they are very high when the length of the growing season (ca. 120 days at most) is considered. Estimates of net community production were first made by Bates et al. (1996) based on carbon budgets, and others have done similar estimates or used nitrogen to estimate seasonal production and export (Smith and Asper, 2000, 2001; Sweeney et al., 2000a,b). These annual estimates of biomass production have resolved the magnitude of the biogeochemical pathways during a single year. However, to date direct observations designed to assess interannual variability of net community production are unavailable.

The physical forcing of the Ross Sea structures the biogeochemical cycles of the region. The generalized current pattern consists of a strong current that follows the contours of the shelf break; on the shelf currents flow along the coast of Victoria Land, and also form gyres that roughly follow the bathymetry (Jacobs and Giulivi, 1998; Dinniman et al., 2003; Smith et al., in press). Cross-shelf exchanges with the Antarctic Circumpolar Current also occur at bathymetric discontinuities and result in the movement of Modified Circumpolar Deep Water (MCDW) onto the shelf. The MCDW waters are relatively warm and likely play a role in the maintenance of the Ross Sea polynya; however, the strength and duration of these intrusions are unknown. Recently large icebergs have calved off the Ross Ice Shelf and grounded in various locations on the continental shelf. In addition to altering the surface advection of ice (Arrigo et al., 2002), they also have modified significantly the currents for relatively long periods (years). The changes in currents, as well as the observed variations in ice cover (Kwok and Comiso, 2002), have the potential for creating marked variations in biological processes on a variety of time scales.

The Ross Sea, like the rest of the Antarctic, is characterized by extreme seasonal changes in physical, chemical and biological processes. Smith et al. (2000) showed that phytoplankton photosynthesis, production, growth and biomass had distinct seasonal patterns, and that each variable was temporally uncoupled from the others. It also was concluded that seasonal patterns were significantly greater than interannual trends. Furthermore, growth appeared to be controlled by irradiance in spring and micronutrient concentrations in summer, whereas loss processes largely controlled biomass. No determination of the effects of assemblage composition to losses or vertical flux was made.

Nutrient and pigment data for the Ross Sea have been compiled, and a monthly climatology of nitrate, silicic acid and chlorophyll concentrations generated using objective techniques (Smith et al., 2003a). This climatology confirmed results from individual cruises that suggested that the major portion of nitrate uptake occurred during austral spring, whereas most of the silicic acid uptake occurred in summer (Nelson et al., 1996; Smith and Gordon, 1997). Because all members of the phytoplankton influence nitrate concentrations, but only diatoms modify silicic acid levels, the seasonal patterns of net community production can be roughly partitioned into major functional groups (that is, diatoms and the haptophyte *Phaeocystis antarctica*). It appears that the growth of *P. antarctica* in the southern Ross Sea occurs in large part in the central portion of the Ross Sea polynya, begins in November, and reaches a biomass maximum in late December, whereas diatomaceous growth occurs both in the eastern and western sections near ice edges and is maximal in January and early February. Unfortunately, few seasonal data exist to adequately resolve the spatial and seasonal patterns suggested by the climatology.

This paper reports the results of a series of cruises completed in the southern Ross Sea during 2001–2004. Nutrient data were collected from within transects of largely ice-free regions, and simple, one-dimensional nutrient budgets were made using nitrogen and silica concentrations. From these budgets diatom and total phytoplankton net production were estimated and compared to the known distribution of phytoplankton. Finally, export was calculated by a comparison of the particulate matter distribution in the upper 200 m with that of nutrient disappearance in order to contrast this estimate with those of other years determined by either nutrient budgets or direct collections of flux.

2. Materials and methods

2.1. Field work

Water samples were collected from the southern Ross Sea during 3 years (2001–2004) in late spring (mid- to late December) and late summer (mid-February) using the *USCGC Polar Star*. Station locations were part of a transect that was roughly parallel to the Ross Ice Shelf, but were largely chosen to sample ice-free waters (Fig. 1A,B). During 2002–2003 little water sampling could be accomplished because of heavy ice conditions and logistical difficulties, so that water was collected at only two stations using the *RVIB N.B. Palmer* during late February. Water was sampled using 10-l Niskin bottles mounted on a rosette frame, which also housed a SeaBird 911+ CTD, a Chelsea fluorometer, photosynthetically active radiation sensor (Biospherical), and a 25-cm WetLabs transmissometer to collect continuous profiles of temperature, salinity, irradiance, fluorescence and suspended particle abundance during water sampling from discrete depths. Sampling depths were

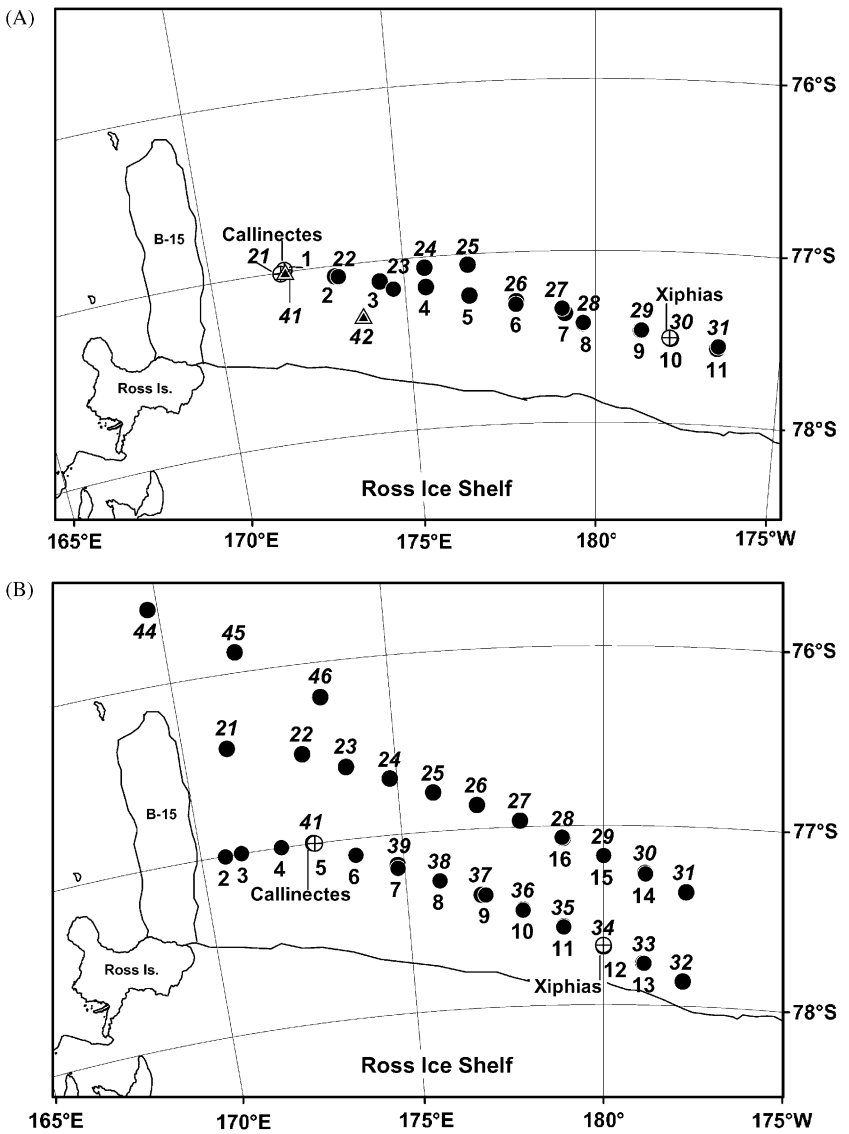

Fig. 1. Maps showing the distribution of the station locations during the three field seasons. (A) Stations from 2001 to 2002 are solid circles, stations from 2002 to 2003 are triangles. Open circles with crosses inside are the locations of the moorings (*Callinectes* and *Xiphias*). (B) Stations from 2003 to 2004, with open circles with crosses inside are the locations of the moorings.

200, 150, 125, 100, 80, 60 and 0 m, along with the 50%, 25%, 15%, 10%, and 1% depths of incident irradiance penetration (total of 12 depths per station). Temperature, salinity and derived density data were binned into 1-m intervals, and mixed-layer depths derived from the vertical distribution of density (Z_{mix} was defined as the depth where σ_T changed by 0.1 units from a stable, surface value; Smith et al., 2000). Complete hydrographic data are available at Smith Jr., 2005; http://www.vims.edu/bio/ivars/. Two moorings also were deployed along the transect: *Callinectes* was the westernmost mooring, and *Xiphias* was the easternmost. Both had WetLabs (Corvallis, OR) in situ fluorometers placed at 19, 25 and 41 m, as well as time-series sediment traps at 200 m (data not reported).

Samples were collected for nutrients (nitrate + nitrite, silicic acid, phosphate), chlorophyll (size fractionated: $<5\,\mu m$, $>20\,\mu m$, and total), pigments, particulate organic nitrogen (PON), and biogenic silica (BSi). Samples (60 ml) for nutrients with elevated chlorophyll levels (those with approximately $1.0\,\mu g\,l^{-1}$ chlorophyll a or more) were filtered through Gelman Acrodiscs (5.0 μm) and frozen at −80 °C for later analysis using standard, automated techniques. Low biomass samples were not filtered. Chlorophyll samples were filtered through either polycarbonate (20 or 5 μm; Poretics) or Whatman GF/F filters, placed in 7 ml 90% acetone, and sonicated for 15 min. After extraction for at least another 15 min on ice in darkness, the filter was removed and the sample read on a Turner Designs Model AU fluorometer before and after acidification. The fluorometer was calibrated before and after the cruise using commercially purified chlorophyll (Sigma) and checked using high-performance liquid chromatography. Particulate organic nitrogen was determined by filtering known volumes of water through precombusted GF/F filters, rinsed with ca. 5 ml 0.01 N HCl in seawater, and drying the filters in combusted glass vials at 60 °C. Blanks were filters placed under the deep-water sample's filter; these filters were processed identically to the other samples. All filters were combusted using a Carlo–Erba Model 254 elemental analyzer (Smith et al., 1996). Samples for biogenic silica were filtered through 0.6-μm Poretics polycarbonate filters, dried in plastic Petri dishes at 60 °C, and returned to the laboratory. The samples then were digested in NaOH at 100 °C for 40 min, neutralized and analyzed colorometrically for reactive silicate on a dual-beam spectrophotometer (Brzezinski and Nelson, 1989). Contributions of lithogenic Si to total BSi are small in the Ross Sea (<1%; Nelson, unpublished) and are ignored.

Samples for pigment analyses (from 0.25 to 2.0 l) were filtered through GFF filters under low vacuum, and flash-frozen in liquid N_2 and stored at −80 °C until analyzed. The filters were placed in 90% acetone in a 1.5-ml microcentrifuge tube, sonicated for 15 min in an ice-water slurry, and extracted in the dark at −20 °C for at least 24 h. The pigment extract was transferred to a second tube and centrifuged for 3 min at 14,000 rpm. Aliquots of the centrifuged extract were diluted with Milli-Q water for analysis. Photosynthetic pigments and pigment-specific activity were quantified using a Waters Spherisorb ODSU C-18 HPLC column and Waters HPLC system (Waters 600 controller and pump with 1000 μl sample loop, Waters 474 scanning fluorometer detector, and Waters 996 photodiode array detector). The separation scheme utilized the following HPLC-grade solvents: solvent A consisted of 85% methanol:15% ammonium acetate (pH 7.5) buffer (v/v; 0.5 M ammonium acetate), solvent B was made up of 87.5% acetonitrile:12.5% Milli-Q water (v/v), and solvent C was 100% ethyl acetate. The following pump gradient was used: 0 min, 95%A, 5%B; 1 min, 100%B; 11 min, 78%B, 22%C; 27.5 min, 10%B, 90%C; 29 min, 100%B; and 30–35 min, 95%A, 5%B. Solvent flow rate was kept at $1\,ml\,min^{-1}$ (Jeffrey et al., 1997). Pigment peaks were identified using Waters Millenium® Chromatography Manager 3.05.01 or Waters Empower Pro software by comparing absorption spectra and elution time to pigments of known absorption spectra and elution times (Jeffrey et al., 1997). Certain pigments were incompletely resolved due to overlaps in elution peaks (e.g., chlorophyllide a peak overlapped chlorophyll *c*3 peak), leading to a possible underestimation of these pigments. Chlorophyll *c*1 and chlorophyll *c*2 were incompletely separated (only one peak was distinguishable) and were considered as one (chlorophyll *c*1 + *c*2).

Two different Waters Spherisorb ODSU HPLC columns were used for calibration and data collection. The two columns were intercalibrated by running known volumes of the same sample on both columns and using area under pigment peaks to determine conversion factors between HPLC columns. The first column was calibrated for photosynthetic pigments using the three-point calibration method; the second column was calibrated using

gradually increasing concentrations of pigment within the expected range. Purified pigments were obtained from pure cultures or mixed phytoplankton assemblages. Pigment concentrations were determined using a Perkin-Elmer Lambda 25 UV/VIS Spectrophotometer and known extinction coefficients.

2.2. Data analysis

The basic method we used to assess net community production is similar to that used by Bates et al. (1998), Smith and Asper (2000) and Sweeney et al. (2000a). Because two, discrete periods were sampled, the temporal dynamics of nutrient uptake could be more completely assessed and related more closely to assemblage composition. Specifically, nitrate uptake was related to net community production at each sampling by

$$\Delta(NO_3^-) = \int_0^z \left(NO_3^-\right)_{\text{winter}} dz - \int_0^z \left(NO_3^-\right)_{\text{min}} dz, \quad (1)$$

where z is depth, and the subscripts min and winter refer to the minimum observed nitrate concentrations observed in the water column and the winter nutrient concentration, respectively. The nitrogen units were converted to carbon units using the measured molar C/N ratio of particulate matter; all integrations were from 0 to 200 m. An integration depth of 200 m was chosen because this is below the depth of nutrient removal during austral summer, and flux to greater depths can be considered to be "lost" from the surface layer on at least seasonal time scales. Similarly, the production of diatoms was estimated using

$$\Delta(Si(OH)_4) = \int_0^z \left(Si(OH)_4^-\right)_{\text{winter}} dz - \int_0^z \left(Si(OH)_4\right)_{\text{min}} dz \quad (2)$$

and converted to carbon units using the molar C/Si ratio (1.61) measured by Nelson and Smith (1986) for blooms overwhelmingly dominated by diatoms. There are no data to suggest that winter values change on decadal scales, and vertical mixing during winter makes nutrient concentrations uniform throughout the water column. Hence, they can be reliably predicted from the AESOPS and RSP[2] data (e.g., nitrate values are 31.0 μM when normalized to $S = 35$ psu, and silicic acid values are 80 μM; Smith and Asper, 2000; Anderson and Smith, 2005; http://usjgofs.whoi.edu/jg/dir/jgofs/southern/). Nitrate potentially can be remineralized within the growing season via nitrification, but this process is extremely slow at the low temperatures of the Ross Sea and can be ignored (Karl et al., 1996). Integrated NH_4^+ concentrations are less than 5% of the total inorganic nitrogen concentrations at all times, and are ignored for these calculations. The particulate nitrogen and silicon distributions were measured, and integrated values compared to the nutrient removal values; the difference was taken to be an estimate of export, although we realize that for nitrogen some portion of the material may have entered the dissolved organic nitrogen (DON) pool. All assumptions used in the calculations are discussed in Smith and Asper (2000). Phosphate was not treated in this analysis due to a more limited particulate phosphorus data set.

CHEMTAX was used to estimate taxa abundances from chlorophyll and carotenoid pigments (Mackey et al., 1996; Wright and van den Enden, 2000). The procedure estimates the contributions of different phytoplankton taxa to the pigment and/or chlorophyll a concentrations via factor analysis and a steepest descent algorithm to find the best fit to the data based on an initial estimate of the pigment ratios. Two main assumptions are made: (1) pigment ratios within any group are constant over the domain encompassed by the data set, and (2) variations in the abundance of different algal groups are not correlated (Goericke and Montoya, 1998). Studies have shown a dependence of cellular chlorophyll a concentrations on environmental and physiological parameters, such as irradiance, growth rate, and nutrient stress. Goericke and Montoya (1998) recommend using regression analysis only for those accessory pigments whose concentrations covary tightly with chlorophyll a, and for this reason we have concentrated on fucoxanthin (a diatom accessory pigment) and 19′-hexanoyloxyfucoxanthin, a pigment found in *Phaeocystis antarctica*. Although other *Phaeocystis* species may contain fucoxanthin (van Leeuwe and Stefels, 1998), this does not appear to be true for the Antarctic form found in the Ross Sea (DiTullio and Smith, 1996; DiTullio et al., 2003). The pigment ratios determined by DiTullio et al. (2003) were used to account for differences in environmental conditions.

Student t-tests (unpaired) between different years and seasons on a variety of hydrographic variables were completed with the level of significance set a priori at $\alpha = 0.05$. Analysis of variance (ANOVA)

was used to compare mean abundances in samples collected from different periods. Where a significant difference was detected for an ANOVA ($p<0.05$), Tukey's multiple comparison test was used to test for specific differences.

3. Results

3.1. Field observations

Ice concentrations and distributions varied markedly in both time and space among the 3 years (Fig. 2). In 2001–2002 ice distributions were similar to the mean condition for the region (Kwok and Comiso, 2002), but 2002–2003 was characterized by both anomalous distributions as well as extremely high concentrations in late summer because of the presence of a large iceberg (C-19) that restricted advective movement of the pack ice to the north. The Ross Sea polynya in spring and summer was much smaller than usual; in addition, the southern Ross Sea became completely ice covered in mid-February, nearly 1 month earlier than normal (which was the major reason we were unable to

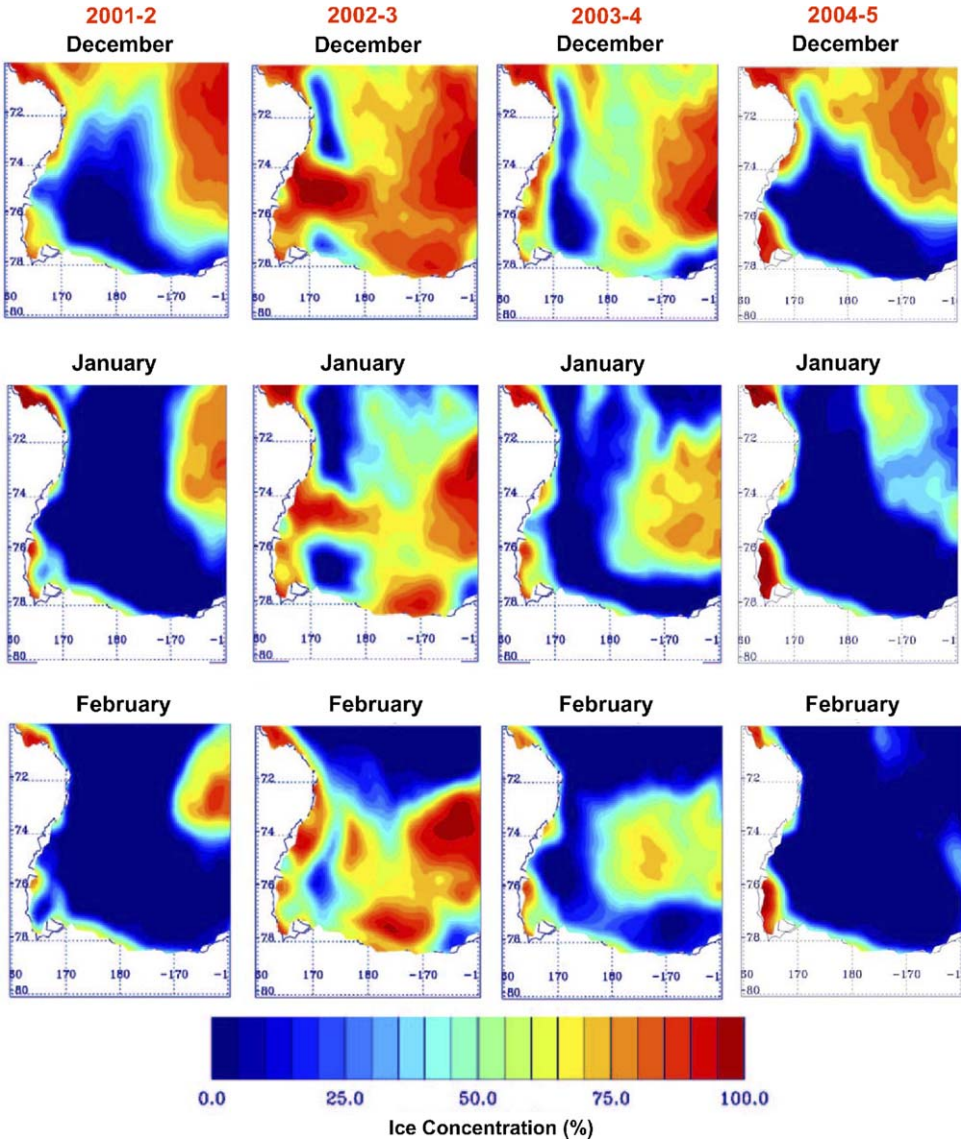

Fig. 2. Ice concentrations and distributions in mid-December, mid-January and mid-February in 2002, 2003 and 2004. Data courtesy of the National Snow and Ice Center.

Table 1
Means and standard deviations of hydrographic data collected during 2001–2002, 2002–2003, and 2003–2004

Year	n	December Z_{mix} (m)	February Z_{mix} (m)	$T_{surface}$ (°C)	$S_{surface}$	σ_T (surface)	σ_T (50 m)	σ_T (150 m)
2001–2002	17	24±8.8	37±14[a,b,c]	−0.64±0.30[b]	34.31±0.07[b]	27.58±0.06[b]	27.63±0.07[d]	27.76±0.05
2002 –2003	2	34±9.7	52±5.7	−1.82±0.05	34.09±0.02	27.44±0.02	27.45±0.04	27.80±0.01
2003–2004	27	19±8.6	20±11	−0.95±0.39	33.89±0.15	27.26±0.11	27.55±0.11	27.74±0.09

The number of measurements (n) refers to the February study. Surface means reflect all samples within the surface layer (1-m binned averages). Data from 2002 to 2003 were not used in statistical analyses due to the low number of stations.
[a]Significantly different from December 2001 to 2002 (Student's t-test, $p<0.05$).
[b]Significantly different from February 2003 to 2004 (Student's t-test, $p<0.01$).
[c]Significantly different from February 2001 to 2002 (Student's t-test, $p<0.01$).
[d]Significantly different from February 2003 to 2004 (Student's t-test, $p<0.05$).

collect data along transects during this year). In 2003–2004 ice concentrations were also greater than the long-term mean (Comiso et al., 1993), but the differences were greatest north of 75 °S and to the east of the dateline. The regions near the ice shelf and north of Ross Island were ice-free. There were no significant differences in December mixed-layer depths among the 3 years, but the 2004 February Z_{mix} mean was significantly less than those in either of the two previous seasons. In austral summer 2002 the surface waters were significantly cooler and saltier than in 2004, but deep (150 m) densities were similar and not significantly different (Table 1). Stratification (based on the density differences between the surface and 150 m) was strongest in 2003–2004 and weakest in 2001–2002.

Nitrate distributions indicated that large differences in phytoplankton uptake occurred between 2001–2002 and 2003–2004. In 2001–2002 a majority (78%) of the nitrate removal occurred from the start of the growing season through late December, and nitrate uptake during January and February was substantially reduced (Fig. 3A,B). The minimum nitrate concentration in 2001–2002 was 16.9 μM (mean concentration in the upper 30 m in late summer was 23.1 μM; Table 2). In contrast, nitrate uptake in the summer of 2003–2004 continued at elevated rates, so that the austral spring uptake represented only 31% of the total seasonal removal. The minimum NO_3 concentration observed was 13.5 μM, and the mean concentration from 0 to 30 m was 17.7 μM (Fig. 3C,D; Table 2). Although only two stations were sampled in February 2003, the minimum nitrate concentration observed was 24.7 μM (Fig. 4A). For comparison, the climatological means in December and February for the upper 30 m are 19.1±3.41 and 17.3±1.04 μM, respectively (Table 2). The spring nitrate concentrations were significantly higher in 2001–2002 (ANOVA, DF = 202, $F = 26.1$; $p<0.001$) when compared to the climatology, and also were significantly higher than the 2003–2004 observations. In the summer of both 2001–2002 and 2003–2004, nitrate concentrations were significantly different from the climatology (ANOVA, DF = 270, $F = 38.06$, $p<0.001$; Table 2), but the in situ data of 2003–2004 were lower than the climatology, whereas in 2001–2002 they were higher.

Silicic acid concentrations did not show the same strong spring removal as did nitrate (Fig. 5A–D), with the integrated removal in spring for both years being only 24% and 14% of the total seasonal removal in 2001–2002 and 2003–2004, respectively. During 2001–2002 the minimum silicic acid concentration observed was 50.9 μM, with the mean concentration in the upper 30 m being 57.6 μM (Table 2). Minimum and mean concentrations observed during the 2003–2004 season were 34.8 and 49.9 μM, respectively, and in February 2003 the minimum value was 61.8 μM (Fig. 4B). Despite the heavy ice concentrations observed in 2002–2003, silicic acid removal still averaged nearly 16 μmol l^{-1} in the mixed layer. Si-uptake in the spring and summer of 2001–2002 was significantly less than the climatological mean, but it was significantly more in both seasons of 2003–2004 (ANOVA, DF = 203, $F = 180$; $p<0.001$, and DF = 272, $F = 91.4$, $p<0.001$; Table 2). Thus, the silicic acid removal was much greater (by ca. 19 μM in the upper 30 m) in 2003–2004 than in 2001–2002.

Phytoplankton biomass in spring was inversely related to nitrate, with the large increases spatially consistent with the large nitrate depletions. Chlorophyll *a* concentrations were maximal in spring; in

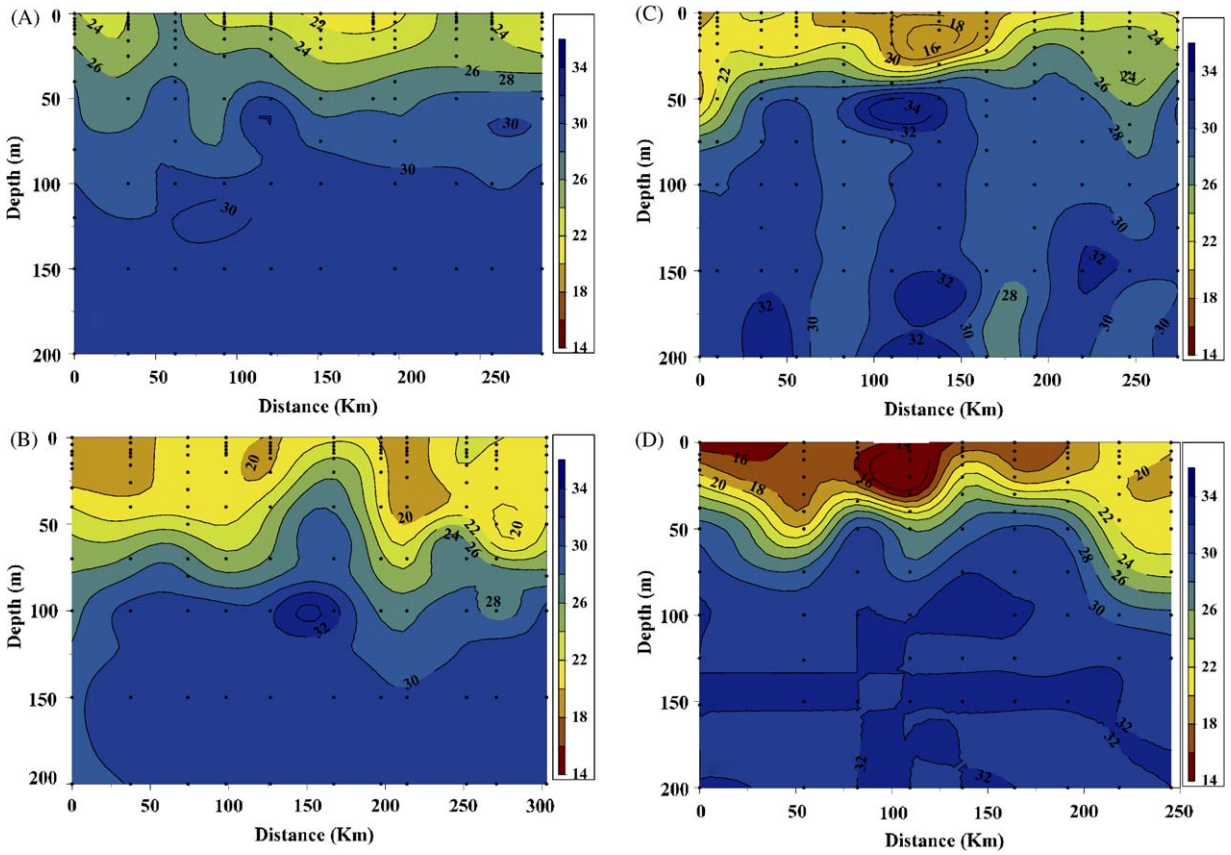

Fig. 3. Nitrate distributions (units = μM) along the southern transect in (A) December 2001, (B) February 2002, (C) December 2003 and (D) February 2004.

Table 2
Mean nitrate, silicic acid and chlorophyll *a* concentrations and standard deviations for the upper 30 m in 2001–2002, 2003–2004 and for the climatology (Smith et al., 2003a)

Year and period	NO_3 (μM)	$Si(OH)_4$ (μM)	Chlorophyll *a* ($\mu g l^{-1}$)
December 2001	$23.1 \pm 2.0^{a,b}$	$77.7 \pm 1.4^{a,b}$	5.86 ± 2.0
February 2002	$20.2 \pm 1.6^{a,b}$	$57.6 \pm 3.21^{a,b}$	$5.61 \pm 1.9^{a,b}$
December 2003	21.8 ± 3.2^{a}	69.1 ± 4.0^{a}	5.74 ± 2.8
February 2004	17.7 ± 3.1^{a}	49.9 ± 7.6^{a}	9.44 ± 3.9^{a}
December climatology	19.1 ± 3.4	73.6 ± 1.7	4.97 ± 1.2
February climatology	17.3 ± 1.0	61.9 ± 2.1	0.99 ± 0.16

[a]Significantly different from the climatology (ANOVA, $p < 0.001$).
[b]Significantly different from 2003 to 2004 (ANOVA, $p < 0.001$).

2001–2002 the maximum in the upper 30 m was $12.1\,\mu g l^{-1}$, and the mean was $5.86\,\mu g l^{-1}$, and in 2003–2004 maximum and mean values were 12.9 and $5.74\,\mu g l^{-1}$ (Fig. 6; Table 2). Maxima in the summers of 2001–2002, 2002–2003 and 2003–2004 were 11.1, 3.84 and $21.3\,\mu g l^{-1}$, and the means in the upper 30 m 5.61, 2.46 and $9.44\,\mu g l^{-1}$, respectively (Table 2; Fig. 4C). In all seasons the percentage of chlorophyll in the $>20\,\mu m$ fraction was $>60\%$ except for spring 2001–2002, when the percentage was 41%. Climatological means for December and February (upper 30 m) averaged 4.97 and $0.99\,\mu g l^{-1}$

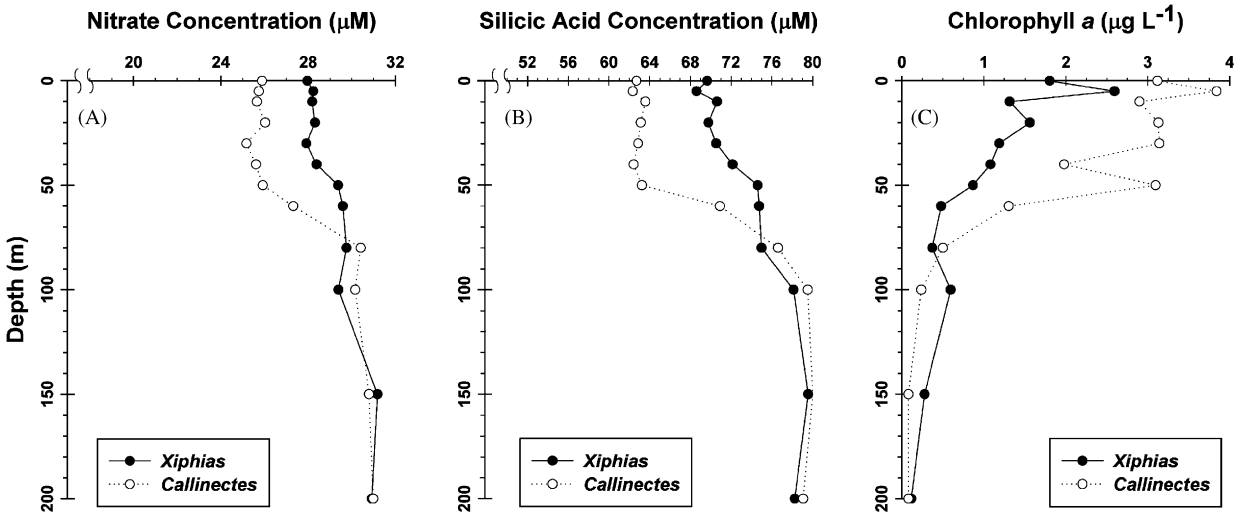

Fig. 4. Vertical profiles of (A) nitrate, (B) silicic acid and (C) chlorophyll *a* on February 21, 2003 collected at 77°32.5′S, 173°58.0′W (*Callinectes*) and 77° 12.9′S, 171° 57.0′W (*Xiphias*) when ice concentrations were near 100% in the southern Ross Sea.

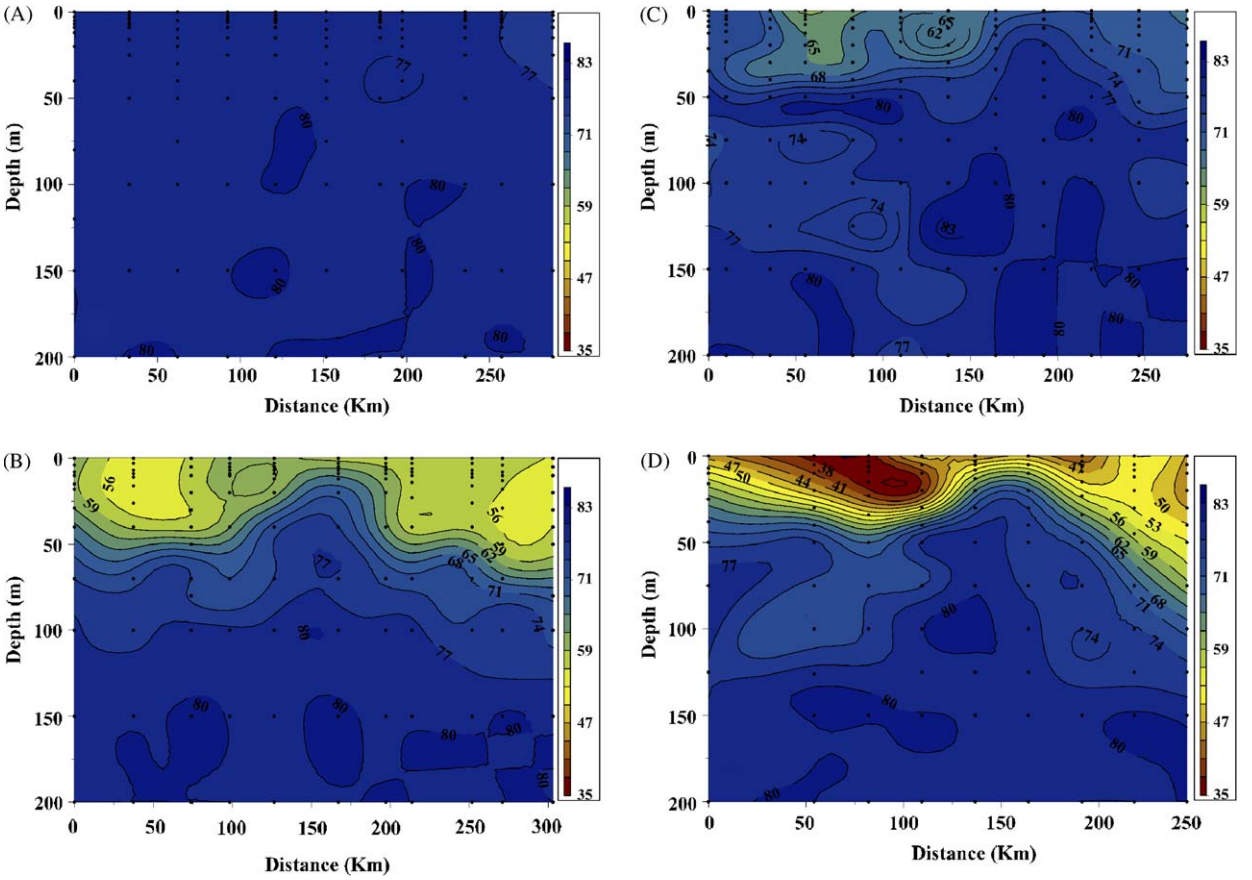

Fig. 5. Silicic acid distributions (units = μM) along the southern transect in (A) December 2001, (B) February 2002, (C) December 2003 and (D) February 2004.

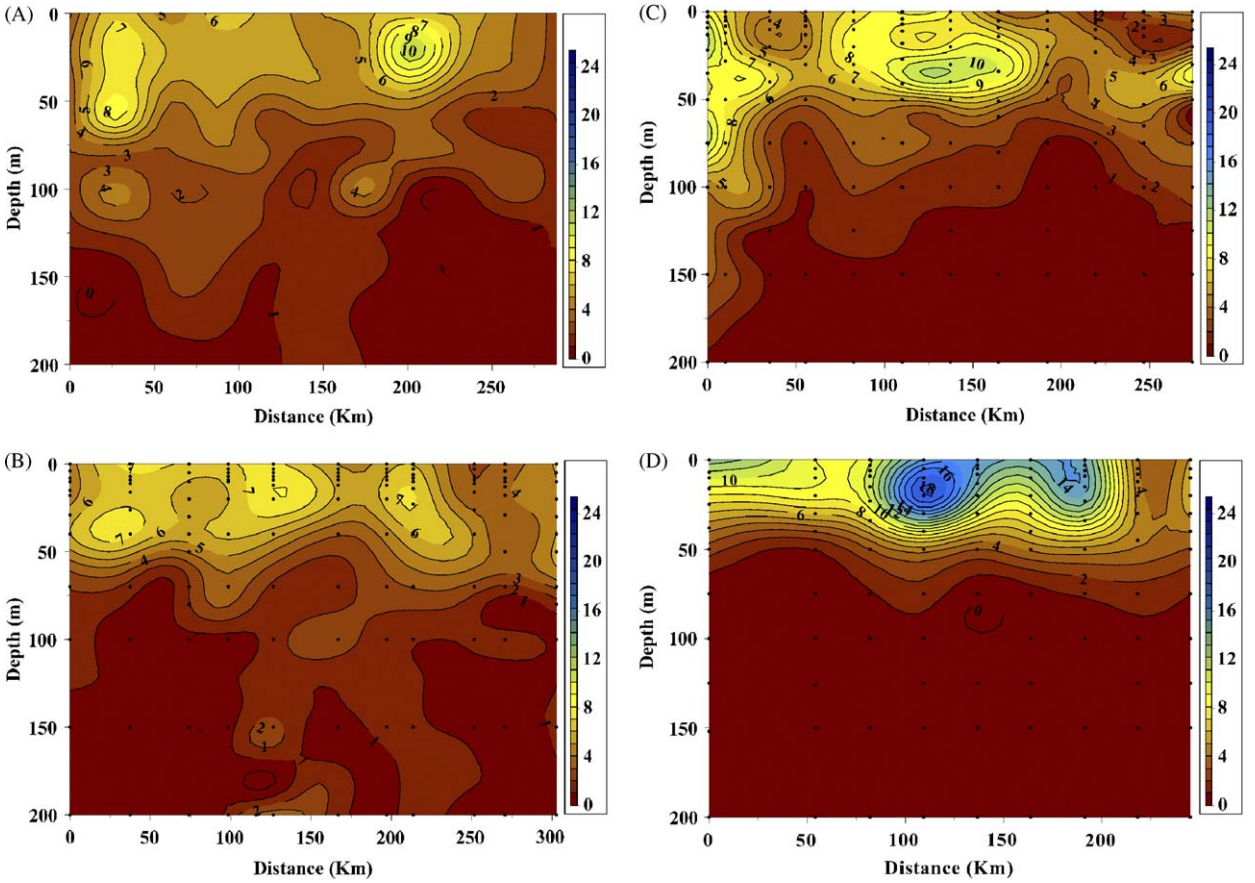

Fig. 6. Chlorophyll *a* distributions (units = $\mu g\,l^{-1}$) along the southern transect in (A) December 2001, (B) February 2002, (C) December 2003 and (D) February 2004.

(Table 2), and the mean in February was significantly lower than the IVARS measurements (ANOVA, DF = 276, $F = 139.9$, $p < 0.001$).

The composition of the assemblages showed substantial spatial and temporal differences. When the contributions to chlorophyll from the southerly transect in 2002 and 2004 were assessed, it was found that diatoms and prymnesiophytes (largely *P. antarctica*) dominated, with a minor contribution of dinoflagellates (less than 10%, except for one station in 2004; Fig. 7). In 2002 the mean diatom chlorophyll contribution was 57% (ranging from 21% to 84%), whereas that of *P. antarctica* averaged 34% (range from 8% to 74%). The larger contribution of diatoms to assemblage composition at the end of 2004 is consistent with the larger silicic acid uptake removal in the euphotic zone.

Measurements of continuous fluorescence in 2003–2004 largely reflect short-term variations in phytoplankton biomass, which in turn are a function of nutrient uptake and loss processes. The fluorescence at the *Callinectes* mooring showed a late-spring (December) maximum throughout the upper 41 m, followed by a uniform decline through mid-January (Fig. 8A). Around 18 January a divergence among depths began, with the surface fluorescence increasing, that at 25 m slightly increasing or staying the same, and that at 41 m continuing to decrease, albeit it at a slower rate. Concentrations at 19 m at the end of the deployment (February 6) were nearly equal to those at the start of the deployment (December 28). In contrast, the moorings at *Xiphias* showed that biomass was low at the time of deployment (December 29), but increased through time at 19 and 25 m (but not 41 m; Fig. 8B). Fluorescence levels at *Xiphias* at the time of recovery were slightly higher than at *Callinectes*, but not substantially. Diel variations at both locations were also evident (amplitude approximately 10% from daily mean, maximum

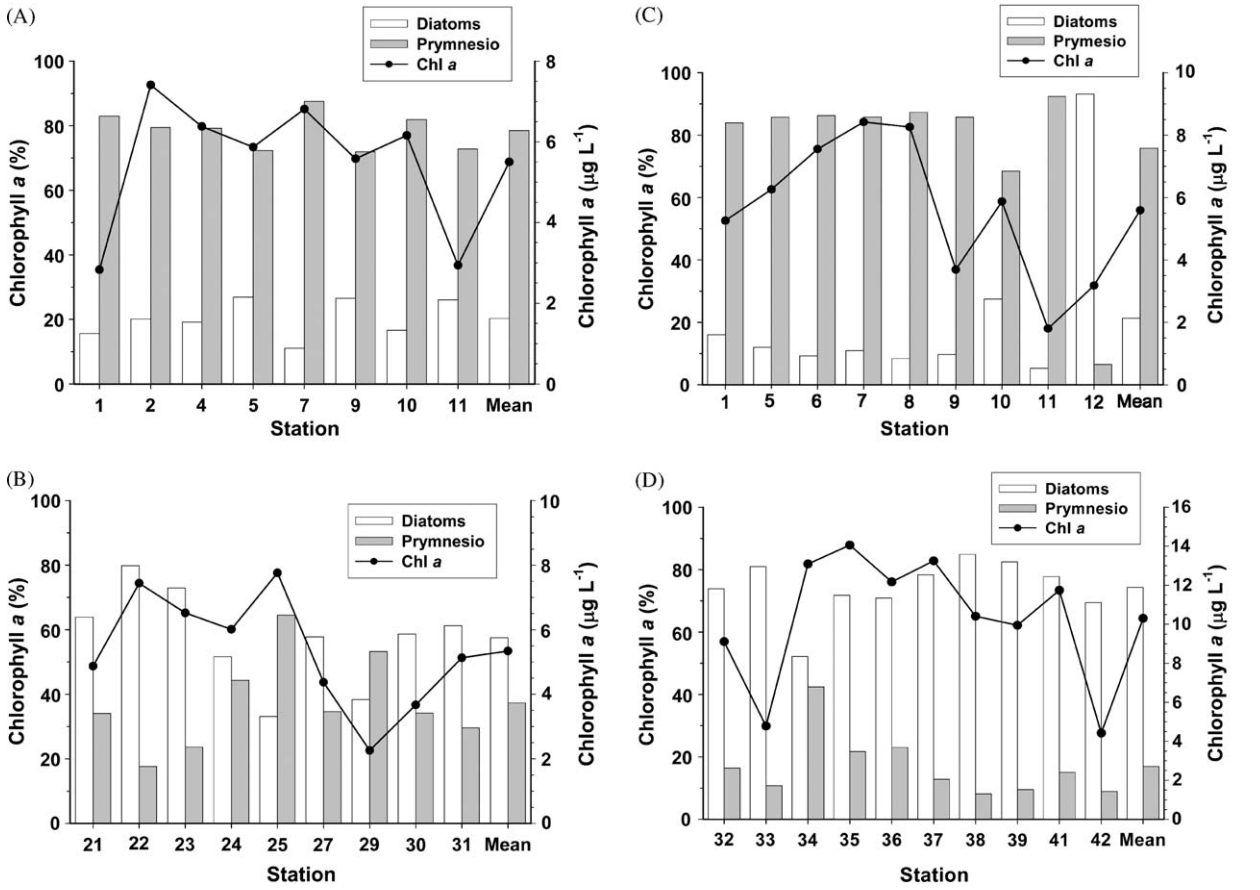

Fig. 7. The percentages of chlorophyll *a* contributed by diatoms and prymnesiophytes along the southern transect in (A) December of 2001–2002, (B) February 2001–2002, (C) December of 2003–2004 and (D) February of 2003–2004 as derived from CHEMTAX analyses using the initial ratios suggested by DiTullio et al. (2003). Mean percentages for the transect are also plotted, as are the mean chlorophyll *a* concentrations in the upper 10 m of each station.

occurring at local noon). Nitrate and silicic acid mixed-layer concentrations as *Callinectes* during February were ca. 15 and 44 μM, whereas at *Xiphias* they were 20 and 52 μM, respectively.

3.2. Nutrient budgets

In spring 2001–2002 the integrated nitrate uptake equaled 0.66 mol m^{-2}, which is equivalent to a November–December productivity of 1.11 g C m^{-2} d^{-1} (Table 3). Similarly, for the entire growing season, the total nitrate removal was 0.85 mol m^{-2}, or productivity over 120 days of 0.70 g C m^{-2} d^{-1}. Summer productivity was thus 0.31 g C m^{-2} d^{-1} (Table 3). In a similar manner, nitrate removal in 2003–2004 for spring, summer and for the entire season equaled 0.54, 1.65 and 2.19 mol m^{-2}, equivalent to a daily carbon productivity of 0.94, 2.71, and 1.82 g C m^{-2} d^{-1}. Silicic acid removal in spring of 2001–2002 was 0.43 mol m^{-2}, and for summer it was 1.38 mol m^{-2} (total net removal for the entire season was 1.81 mol m^{-2}; Table 3). This is equivalent to a diatomaceous productivity for austral spring, summer and the entire 2001–2002 season of 0.19, 0.59, and 0.39 g C m^{-2} d^{-1}. Thus diatoms accounted for only 17% of the productivity in spring, but 55% of the total seasonal productivity. Diatom silicic acid removal in 2003–2004 for spring, summer and the entire year equaled 0.74, 4.68 and 5.41 mol m^{-2}, which when converted to carbon units was 0.32, 1.99, and 1.16 g C m^{-2} d^{-1}, respectively (Table 3). This represents 35%, 73% and 64% of the spring, summer and seasonal production. Although only two stations were sampled in late summer, 2003 (2002–2003 season), the carbon productivities

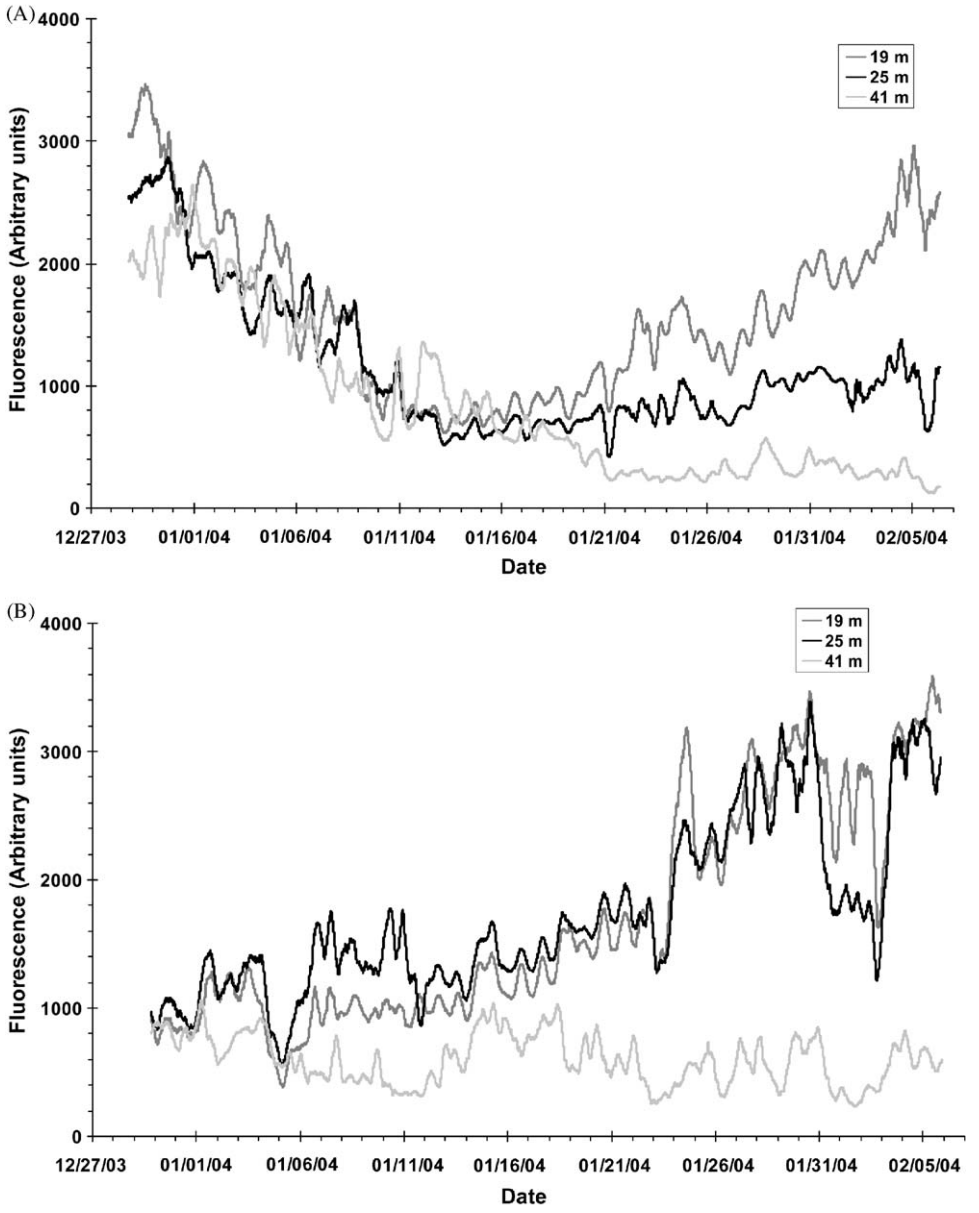

Fig. 8. In situ fluorescence observed during 2003–2004 at three depths (19, 25 and 41 m) and two locations (A: 76° 59.16′S, 172° 42.48′E, and B: 77° 40.93″S, 178° 58.40′W) in the southern Ross Sea. Each line is a running average of 50 consecutive data points. 1000 fluorescence units are approximately equal to $1\,\mu g\,l^{-1}$ chlorophyll *a*.

derived from the nitrogen and silica deficits were equal to 0.018 and $0.015\,mg\,C\,m^{-2}\,d^{-1}$, and diatom production was 84% of the total net community production for the year.

N:Si uptake ratios were calculated using the integrated nitrate and silicic acid removal estimates (Table 4). In 2001–2002, the ratio was low in spring (0.66), but increased by an order of magnitude during summer (to 7.13), so that the seasonal ratio was 2.13. The same ratio estimated from the limited 2002–2003 data gave a ratio of 3.05. Spring, summer and seasonal Si:N uptake ratios in 2003–2004 were 1.36, 2.84 and 2.47.

Because the particulate nitrogen and biogenic silica concentrations were measured at the same depths and locations where nutrients were assessed, it is possible to compare the nutrient removal estimates with the particulate matter concentrations

Table 3
Net nitrate and silicic acid uptake (and standard deviations) of phytoplankton as estimated by Eqs. (1) and (2), and the computed carbon-equivalent production of the entire assemblage and of diatoms

Date and period	Nitrate uptake ($mol\,m^{-2}$)	Carbon productivity ($g\,C\,m^{-2}\,d^{-1}$)	Silicic acid uptake ($mol\,m^{-2}$)	Diatom carbon productivity ($g\,C\,m^{-2}\,d^{-1}$)
Spring, 2001[a]	0.66 ± 0.74	1.11	0.43 ± 0.75	0.19 (17%)
Summer, 2001–2002[b]	0.19[c]	0.31	1.38[c]	0.59 (188%)
Entire Season, 2001–2002[d]	0.85 ± 0.27	0.70	1.81 ± 0.66	0.39 (55%)
Spring, 2003[a]	0.54 ± 0.22	0.94	0.74 ± 0.30	0.32 (35%)
Summer, 2003–2004[d]	1.65[c]	2.71	4.68[c]	1.99 (73%)
Entire Season, 2003–2004[b]	2.19 ± 0.30	1.82	5.41 ± 1.13	1.16 (64%)

Values in parentheses are carbon-equivalents of the diatom production as percentages of total net community production. Molar nitrate uptake was converted carbon by multiplying by the molar ratio of C/N observed during the field season in the upper 50 m and assuming an *f*-ratio of 0.8, 0.7, and 0.75 for the spring, summer and entire season (derived from http://usjgofs.whoi.edu/jg/dir/jgofs/southern/). Silicic acid uptake converted to carbon using the molar Si:C ratio (1.61) observed by Nelson and Smith (1986) and using the same *f*-ratio as for nitrogen.

[a]Growing season assumed to be from November 1 to December 26 (55 days); *f*-ratio assumed to be 0.8 for both nitrogen and silicon.
[b]Growing season assumed to be from November 1 to February 28 (120 days); *f*-ratio assumed to be 0.7 for both nitrogen and silicon.
[c]Calculated by difference.
[d]Growing season assumed to be from December 27 to February 28 (65 days); *f*-ratio assumed to be 0.75 for both nitrogen and silicon.

Table 4
Ratios of integrated nitrate to integrated silicic acid uptake, nitrogen export, and silicon export during spring, summer and the entire season during the three field seasons

Year/season	$Si(OH)_4$:NO_3 uptake (mol/mol)	Nitrogen export ($mol\,m^{-2}$)	Silicon export ($mol\,m^{-2}$)
2001–2002, Spring	0.66	0.16	0.27
2001–2002, Summer	7.13	0.32	0.88
2001–2002, Entire season	2.13	0.48	1.15
2002–2003, Entire season	3.05	—	—
2003–2004, Spring	1.36	0.18	0.58
2003–2004, Summer	2.84	1.75	4.12
2003–2004, Entire season	2.47	1.94	4.70

Export is defined as the difference between the nutrient uptake and the particulate form present.

at that time, and calculate the amount of material that was lost from the upper 200 m either via transformation to reduced, dissolved forms (for nitrogen) or by export from the surface layer as particles. In spring (the period from early November through our sampling in late December) 2001–2002, "export" equaled 0.16 and $0.27\,mol\,m^{-2}$ of nitrogen and silicon, and in summer (the period from late December through our sampling date in February) it increased to 0.48 and $1.15\,mol\,m^{-2}$ (Table 4). In contrast, export in 2003–2004 in spring was 0.18 and $0.58\,mol\,m^{-2}$ for nitrogen and silicon, and in summer 1.75 and $4.12\,mol\,m^{-2}$ (Table 4). Thus, on a seasonal basis silicon and nitrogen export were 4.1 and 4.0 times greater in 2003–2004 than in 2001–2002, respectively.

4. Discussion

4.1. Temporal variations

While a full quantitative assessment of the interannual variations within the southern Ross Sea cannot be derived from the data of these 3 years alone, the observations do indicate the extent and nature of these variations. Comparison of the hydrographic data shows that mixed layer depths increased from December through February in the

first two field seasons (with the increase in 2001–2002 being significant; Table 1), which is similar to the results of Smith and Asper (2001), who found that Z_{mix} was minimal in late December (22.6 m) and increased through January. Smith et al. (2000) found that the minimum Z_{mix} was between mid-December and early January (no sampling occurred between those two dates), and that mixed layer depths increased slightly through February. Mixed layers found from February 2–9, 1997 (26 ± 11) were not significantly different than those we found in 2002 or 2004 during the same period. Mixed layers were not significantly different in December between 2001–2002 and 2003–2004, but were significantly different in February between the two seasons (Table 1), suggesting that either wind mixing or brine rejection was initiated earlier that year than in 2004. Given that temperatures were substantially above the freezing point, we believe that wind mixing was a more likely cause for the differences between years. Increases in mixed-layer depths are not surprising in 2002–2003, as the region was ice covered and some brine rejection-induced vertical mixing had most likely been initiated. Ice and snow cover also increase albedo and decrease the amount of solar heat into the surface layer, thereby reducing stratification. The increase in 2001–2002 may have been the result of episodic wind events, but there are no synoptic meteorological data with which to test that hypothesis. Mixed layers near 40 m are close to the maximum suggested by Mitchell and Holm-Hanson (1991) as being the deepest mixing that would still support positive community photosynthesis, and so it is quite possible that at some of the stations light limitation of phytoplankton growth was occurring.

There was no apparent relationship between large-scale ice distribution and interannual variations in phytoplankton biomass and assemblage composition. In 2001–2002 ice concentrations were "normal" and similar to the long-term trends with regard to the timing of rapid ablation and the area uncovered (Kwok and Comiso, 2002), and gave rise to a high biomass, *P. antarctica*-dominated bloom in spring followed by an assemblage in which diatoms contributed a majority of the chlorophyll. In 2003 ice concentrations were extremely heavy, and the February assemblage appeared to be dominated by diatoms. Finally, 2003–2004 was a heavy ice year, with reduced open-water concentrations in all regions (and especially near 75 °S, 170 °W, both on and off the continental shelf), but with a large *P. antarctica* bloom in spring and a secondary, very large diatom bloom by February (Table 2). Indeed, the secondary bloom was an order of magnitude greater than the February climatology. It has been frequently suggested that *P. antarctica* is favored under low-irradiance conditions (via deeper mixed layers) when compared to diatoms (Moisson and Mitchell, 1991; Arrigo et al., 1999; Smith and Asper, 2001); however, on the coarse scale of our analysis, ice cover (and hence irradiance) did not seem to consistently structure assemblage composition. We sampled ice-free waters more completely, and so the generalized description of assemblage composition refers only to those waters with low ice concentrations. It does suggest, however, that irradiance is only one factor controlling biomass and composition of the Ross Sea phytoplankton.

Nitrate concentrations during the 3 years varied substantially, and the resultant February concentrations in the surface layer ranged from 13.7 to 26.9 μM. In 2003–2004 the mean nitrate concentration was significantly less than either the climatology or the in situ levels found in the previous two field seasons, whereas the means in 2001–2002 and 2002–2003 were greater than the climatology. Variations in silicic acid were also significantly different from the climatology, with spring 2001 concentrations being greater, but with the concentrations in summer 2001–2002, spring 2003–2004, and summer 2003–2004 being less. The mean concentration in 2003–2004 was also significantly less than in 2001–2002. This suggests that silicic acid removal in 2001–2002 in spring was reduced relative to the long-term mean, but it continued and did not decrease as much as might have been expected in summer. Silicic acid uptake in 2003–2004 was substantial throughout the year. We believe that the variations in relative nutrient uptake can be best explained by variations in assemblage composition effects, but also are influenced by variations in N/Si uptake ratios. Changes of assemblage composition potentially could alter both food webs (as it has been suggested that *P. antarctica* is largely ungrazed and is remineralized within the water column; DiTullio and Smith, 1996; Caron et al., 2000) and biogeochemical cycles.

Data from other studies collected in approximately the same area can be directly compared to these. Smith and Asper (2001) found the mean nitrate and silicic acid concentration during late December 1995 to be 20.7 and 63.4 μM (both

significantly less than those in 2001), with minima being 12.5 and 51.6 μM, respectively. Mean NO_3 concentrations in 1997 were 12.5, which were significantly less than in 2001/2002, but were similar to those measured in 2004. Clearly substantial interannual variations in nitrate concentrations occur as a result of variations in the uptake of nitrate by phytoplankton, and hence the question then arises as to the causal mechanism of these differences.

4.2. Nutrient budgets

Removal of nitrate and silicic acid varied substantially among years and seasons. Nitrogen uptake in spring was similar between the 2 years (0.66 and 0.54 mol m^{-2}), but the uptake in summer was far greater in 2003–2004 (1.65 vs. 0.19 mol m^{-2}, more than an 8-fold increase). Silicic acid uptake was also similar between the 2 years (0.43 vs. 0.74 mol m^{-2}) in spring, but again summer differences were extreme, with 2003–2004 having a much greater uptake than 2001–2002 (4.68 vs. 1.38 mol m^{-2}, 3.4 times as much; Table 3). The difference only can be explained by a different biological removal, which in turn must have been related to both overall controls of productivity as well as the types of phytoplankton taxa present.

Uptake ratios of silicon:nitrogen can be affected by two independent factors: influence by non-siliceous phytoplankton on the uptake of nitrogen, and alteration of the Si:N uptake ratio by trace metal limitation. One of the major phytoplankton species in the southern Ross Sea is *Phaeocystis antarctica*, and its presence would result in a removal of nitrate in the absence of the removal of silicic acid. As *P. antarctica* often is found in substantial quantities in spring, $Si(OH)_4$:NO_3 uptake ratios would be expected to be relatively low. Hutchins and Bruland (1998) and Takeda (1998) found that iron limitation elevates the $Si(OH)_4$:NO_3 uptake by suppressing nitrate uptake while silicon uptake proceeds at relatively normal rates. Furthermore, iron limitation has been experimentally observed in the southern Ross Sea by a variety of means (Sedwick and DiTullio, 1997; Sedwick et al., 2000; Olson et al., 2000). Our $Si(OH)_4$:NO_3 uptake ratios were low (less than or equal to 1) in spring, consistent with both the large contribution of *P. antarctica* and the absence of iron limitation. However, uptake ratios increased in both summers (Table 4), and in 2001–2002 the ratio exceeded 7 (in nutrient replete cultures the ratio is near 1; Takeda, 1998). Such elevated ratios are commonly found only in highly iron-stressed systems, and we suggest that in the summer of 2001–2002 low levels of iron limited the diatom assemblage. Growth did not cease, as evidenced by the continued (albeit slow) reduction in nitrate (by nearly 3 μM during summer in the surface layer), but it clearly was substantially reduced. *P. antarctica* could not have replaced diatoms, as its iron requirements appear greater than those of the diatoms of the region (Coale et al., 2003); indeed, it is possible that iron limitation and stress of *P. antarctica* may be a cause for increased losses due to passive sinking of colonies, aggregation, and disruption of colonies (Smith and Asper, 2001; Smith et al., 2003b).

The Si:N uptake ratio in summer 2003–2004 increased to 2.84, which also indicates the potential for iron-stress, but we suggest that the growth of diatoms was not greatly influenced and that they continued to increase in biomass. Summer nitrate uptake was nearly an order of magnitude greater than in summer 2001–2002 (Table 4); furthermore, fluorescence decreased in mid-January at *Xiphias*, but then increased to levels comparable to those found in the December maximum (Fig. 8A,B). Chlorophyll levels also were higher in February when compared to December (Table 2). We believe diatoms largely drove this increase. Such a substantial and unexpected increase (based on the climatological chlorophyll distribution, which decreases during February; Table 2) suggests that iron limitation was not great enough to reduce greatly growth, and as such, suggests that iron inputs to the region may have been greater in 2003–2004 than in 2001–2002. Although the hydrographic data from 150 m do not contain anomalous data, a more detailed analysis of the data from 50 to 200 m show pockets of what appears to be modified circumpolar deep water (Peloquin, 2005). MCDW may be a source of heat and iron and is characterized by being warmer (~−0.5 °C), more saline (~34.4–34.5) and relatively micronutrient-rich compared to surrounding waters (Hiscock, 2004). The intrusion of MCDW onto the Ross Sea continental shelf has been reported previously (Jacobs et al., 1985), and has been suggested to influence the timing and magnitude of the seasonal phytoplankton bloom by providing iron to surface waters (Hiscock, 2004; Arrigo and van Dijken, 2004). A criticism of this hypothesis is that stratification was still strong in February, which would restrict the introduction of the Fe-replete

waters to the euphotic zone. However, in a fine-resolution study Hales and Takahashi (2004) detected small expressions of this water mass in Ross Sea surface waters, suggesting that mesoscale inputs of iron occur and may fuel blooms. Therefore, we believe that the initial *P. antarctica* accumulation and growth was fueled by iron supplied via deep winter mixing, and that the secondary bloom dominated by diatoms was initiated by the introduction of MCDW into the euphotic zone.

Export of biogenic material from the surface layer (200 m), calculated by mass balance, also showed substantial differences among years (Table 4). Nitrogen disappearance was 4-fold greater in 2003–2004 than in 2001–2002 for the entire season, although in spring the export was only 2.1-fold greater. For silicon the differences in export were nearly exactly the same. Comparison with the observations of Sweeney et al. (2000b) indicates that 1996–1997 had a nitrogen reduction ($1.33\,mol\,m^{-2}$) intermediate between 2001–2002 and 2003–2004, whereas the silicon deficit ($0.47\,mol\,m^{-2}$) was more than an order of magnitude less than we observed in 2003–2004. This suggests that diatoms were far more important in the biogeochemical budgets during the period of our observations, even though the exact reasons for these differences cannot be definitively ascertained.

Our seasonal estimates of export can be roughly compared to those obtained by sediment traps. The comparison is inexact, because our estimates are nitrate disappearance rates, and nitrate can be reduced into dissolved pools in addition to reduced particulate pools. By not accounting for DON and NH_4 increases, particulate export is overestimated. DON net production in the upper 150 m was estimated by Carlson et al. (2000) to be ca. 9% of PN production, and ammonium production by mid-January was ca. 2% of PN production (Smith and Asper, 2000), but Gordon et al. (2000) reported late summer NH_4 values that were approximately double those of Smith and Asper (2000). To complicate the budget further, NH_4 is rapidly used by phytoplankton in the surface layer, so that ammonium budgets will underestimate the true fluxes through this pool. Based on these uncertainties, the production of dissolved, reduced N (the sum of ammonium and DON) likely is ca. 20% of particulate production. This is not insignificant, but also is likely to be the maximum influence on the total N budget. Silicon has no reduced phases and is not influenced by the same biological processes.

The particulate flux data of Collier et al. (2000), for the same season as the nutrient deficit results of Sweeney et al. (2000b), show that during austral spring 1996/7, N flux at 206 m was $0.67\,mol\,m^{-2}$, and that Si fluxes were ca. $0.34\,mol\,m^{-2}$ (assuming a C/Si ratio of 0.1 in early season and calculating the flux from November 1). N and Si fluxes through February 8 equaled approximately 3.34 and $3.81\,mol\,m^{-2}$, respectively. These are higher than those estimates of export we made, but it should be noted that in both years we found a substantial amount of biogenic matter still within the water column. Presumably this material ultimately would be either remineralized or contribute to particulate flux to depth. Nearly all sediment traps have detected a significant temporal decoupling between production and vertical flux (Nelson et al., 1996; Smith and Dunbar, 1998; Dunbar et al., 1998; Collier et al., 2000), and our particulate matter distributions and concentrations would suggest that a substantial amount of export (but not regeneration) of nitrogen and silicon would occur after the last period of our sampling.

It remains unclear what the fate of the material exported below 200 m might be. It is possible that the diatomaceous material at that depth will sink rapidly and reach the sediments relatively intact, whereas the organic material in *P. antarctica* might be largely remineralized within the water column (Nelson et al., 1996). Sinking rates of the two forms (siliceous vs. non-siliceous) are likely different (both at the surface as well as at depth), as is the time of appearance in the surface layer. The composition of the surface assemblage influences the material collected in traps at depth (Dunbar et al., 1998), but our results do not extend long enough to the contributions resolve adequately of the quality of surface biogenic material vs. the absolute export.

4.3. Spatial variations

An assessment of interannual variations can be obscured by spatial variations. All studies of biomass in the Ross Sea have observed variations not only in phytoplankton biomass, but in assemblage composition, and these variations occur on a variety of scales (Hales and Takahashi, 2004). Many of the spatial variations may indeed be coupled to temporal variations; that is, the time needed for biomass changes is dependent on the spatial distribution of a primary physical constraint like ice (Arrigo et al., 1998). Measurement of fluorescence

at one location through time (Fig. 8) provided a high-resolution time series that clearly documented the increases and decreases in biomass and provided insights into the causal mechanisms for these changes. For example, at site *Callinectes* in the eastern portion of the study area, biomass was high upon deployment of the mooring, and began to decrease through mid-January. This parallels prior observations that observed that the *P. antarctica* bloom peaks in mid-December and then is reduced due to biologically mediated loss processes (reduced growth, aggregation and rapid passive sinking to depth with remineralization; Smith et al., 2000; Smith and Asper, 2001; Asper and Smith, 2003). The secondary peak is far more unusual for the Ross Sea proper, although such February maxima have been observed in Terra Nova Bay (Nuccio et al., 1999). The bloom is also associated with a strong silicic acid draw-down (removal of ca. 36 μM $Si(OH)_4$), and therefore we conclude that it was largely consisted of diatoms. In contrast, the site *Xiphias* was relatively low in biomass upon deployment of the fluorometer, but increased with time. This increase also was largely diatom-dominated, as evidenced by the removal of ca. 28 μM of $Si(OH)_4$. The western area of the study region is much more strongly influenced by ice (Fig. 2), and since diatoms are often associated with areas of strong ice ablation (Arrigo et al., 1999), the presence of diatoms at *Xiphias* is not surprising. Again, the unusual aspect of this bloom is the absolute magnitude.

Advection of water could introduce a serious error into our calculations of nutrient drawdown. However, we do not believe that this error was substantial during this time period. Measured net velocities within our study area are ca. 0.6 and 1 cm s^{-1} (220 and 440 m) when measured throughout the year, and even less during summer (Pillsbury and Jacobs, 1985; Picco et al., 1999). Such rates represent a monthly advection of 15.6 and 25.9 km and clearly are small relative to the size of the observed bloom (100's of km; Smith and Nelson, 1985; Arrigo et al., 1999). Similar calculations of transport based on modeled results confirm the relatively minor advective motions (Dinniman et al., 2003). Advective changes large enough to alter the nutrient budgets also should be observed as rapid changes in the continuous record of fluorescence (Fig. 8); however, none were observed during 2003–2004. While advection might introduce errors in our calculations, we have no evidence to suggest that this is a significant error in our budgets.

5. Conclusions

Variations among years in the biogeochemical variables and cycles of the southern Ross Sea are large. All 3 of the years we sampled were in some ways anomalous when viewed in the context of the long-term conditions of the region (Smith et al., 2003a). Arrigo et al. (1999) suggested that if climate change were to increase the stratification of the Ross Sea that diatoms would likely replace *Phaeocystis antarctica*. However, ice concentrations are significantly increasing through time in the Ross Sea (Kwok and Comiso, 2001), which would potentially decrease stratification and irradiance, conditions that would favor *P. antarctica* (Arrigo et al., 1999). It is impossible to say if the large diatom blooms observed in February 2004 will be a consistent feature in the future, but we do know that these diatom accumulations were much greater than was observed in studies conducted during the 1990s (Arrigo et al., 1999; Smith et al., 2000). Because phytoplankton assemblage composition has such a critical role in both food web structure and biogeochemical cycles, knowledge of this variable is critical to our understanding of energetic and elemental cycles of the Ross Sea. Further measurements are needed to establish the role of iron and grazing on phytoplankton composition and biomass in the region. Only with additional time series measurements can we begin to understand and predict the interannual variability and the long-term temporal changes that might occur in the Ross Sea as a result of regional, basin-wide and global change.

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