

Variability in nutrient concentrations around Elephant Island, Antarctica, during 1991–1993

NELSON SILVA S., E. WALTER HELBLING, VIRGINIA VILLAFANE, ANTHONY F. AMOS, and OSMUND HOLM-HANSEN



Silva S., N., Helbling, E. W., Villafañe, V. E., Amos, A. F. & Holm-Hansen, O. 1995: Variability in Nutrient Concentrations around Elephant Island, Antarctica, during 1991–1993. *Polar Research* 14(1), 69–82.

The nutrient status of the various water mass structures within a large sampling grid around Elephant Island are reported and the nutrient concentrations relative to data from the physical and biological components of the Antarctic Marine Living Resources Programme are discussed. Concentrations of silicic acid, nitrate and phosphate (Si/N/P) were measured in the upper water column during January–March of three successive years. Samples were taken from eleven depths at 17 stations in 1991, and at four depths at 144 stations in 1992 and 182 stations in 1993. There was considerable variability in the concentrations of all three nutrients within the study area, but silicic acid showed the greatest variance among the water masses present in the sampling grid. The ratios (Si/N/P) of the nutrient deficits (difference in winter and summer values) in the upper 100 m differed considerably in Drake Passage waters as compared to Bransfield Strait waters, with both nitrate and silicic acid showing the greatest variance. Nutrient deficits did not increase from January to February, indicating that rates of replenishment of nutrients to the euphotic zone by physical processes and/or biological regeneration were approximately equal to the rate of uptake and assimilation by phytoplankton during that time period. The seasonal deficits, however, were substantial. Estimates of daily rates of primary production based on these nutrient deficits were comparable to the rates as measured by radiocarbon for Drake Passage waters, but much smaller for Bransfield Strait waters.

Nelson Silva S., Escuela de Ciencias del Mar, Universidad Católica de Valparaíso, Casilla 1020, Valparaíso, Chile; Walter E. Helbling, Virginia Villafañe and Osmund Holm-Hansen, Polar Research Program, Scripps Institution of Oceanography, University of California San Diego, La Jolla, California 92093-0202, U.S.A.; Anthony F. Amos, University of Texas at Austin, Marine Science Institute, Port Aransas, Texas 78373, U.S.A.

Introduction

Concentrations of nitrate (N), phosphate (P), and silicic acid (Si) in Antarctic waters are generally very high (Le Jehan & Tréguer 1985) due to the combination of strong and continuous upwelling of nutrient-rich Upper Circumpolar Deep Water (UCDW) at the Antarctic Divergence coupled with relatively low rates of biological uptake. The UCDW is associated with a maximum in temperature and phosphorus and nitrogen concentrations (Sievers & Nowlin 1984). The low rate of biological uptake is due to low phytoplankton biomass and to low growth rates induced by temperature restraints on enzymatic rates (Neori & Holm-Hansen 1982; Tilzer & Dubinski 1987). Significant differences in nutrient concentrations and in covariation of nitrate, phosphate, and silicic acid, however, can be documented at various

space and time scales in Antarctic waters (Tréguer & Jacques 1992). It has been shown (Zentara & Kamykowski 1981; Kamykowski & Zentara 1989) that waters to the south and to the north of the Antarctic Divergence can be distinguished on the basis of their nutrient relationships, and it has been suggested that the differences in relative nutrient concentrations may affect food web dynamics. Even within the same water mass, considerable mesoscale patchiness and variability can be detected in surface pelagic Antarctic waters (El-Sayed 1970). The greatest variability and patchiness of nutrient concentrations, however, is generally found in waters over the continental shelf in association with rich phytoplankton blooms that often have chlorophyll- α concentrations of over $20 \mu\text{g l}^{-1}$ (Burkholder & Sieburth 1961; Holm-Hansen & Mitchell 1991). In such rich areas, concentrations of N and P can be depleted to the extent that they are undetectable

by conventional calorimetric methods (Nelson & Smith 1986).

The area around the northern portion of the South Shetland Islands and Elephant Island is interesting with regard to nutrient conditions for phytoplankton, as the region is known to sustain high krill and zooplankton biomass (Amos 1984; Brinton et al. 1987; Macaulay et al. 1984; Nast et al. 1988; Loeb et al. 1993a) and hence is usually assumed to also have high rates of primary production. This area is oceanographically complex as it is a zone of mixing between waters from Drake Passage, the Bellingshausen and Weddell seas, and the Bransfield Strait. Early work by Sverdrup (1933) and Clowes (1934) indicated the presence of different water masses interacting in this general area. More detailed investigations by Gordon & Nowlin (1978), Patterson & Sievers (1980), Sievers (1982), Gordon (1988), Stein (1988), and Sievers & Nowlin (1988) have subsequently shown that there is much temporal and geographical variability in the physical regime. The upper 750 m of the water column is influenced by various water masses (Antarctic Surface Water, Upper Circumpolar Deep Water, Lower Circumpolar Deep Water, Bransfield Surface and Deep waters), each of which shows distinct characteristics in terms of physical and chemical features as described by Gordon & Nowlin (1978), Sievers & Nowlin (1984) and Silva S. (1985, 1986). The major physical characteristics include the presence of important frontal systems (Jacobs 1991; Helbling et al. 1993) between the different water masses. Although various programmes have measured nutrient concentrations in this general area (Silva S. 1985, 1986), the sampling strategy has been too dispersed to permit analysis of nutrient concentrations relative to the physical and biological characteristics of the various water masses which meet and mix in this area.

During the past four years the U.S. Antarctic Marine Living Resources (AMLR) programme has supported a multidisciplinary study of the area around Elephant Island, which has included measurement of inorganic nutrient concentrations in the upper water column over a large sampling grid during January–March of three successive years (1991 to 1993). In this paper we report the nutrient status of the various water mass structures within the sampling grid and discuss the nutrient concentrations relative to data from the physical and biological components of the AMLR programme.

Materials and methods

The AMLR study grid, which was occupied from early January to mid-March of 1991–93, covers approximately $50 \times 10^3 \text{ km}^2$ around Elephant Island (Fig. 1). Each station was occupied two times during each field season (during Leg I in January–February and Leg II in February–March) with a total number of stations being 100 in 1991, 144 in 1992, and 182 in 1993.

A profiling unit, consisting of a General Oceanics rosette with Conductivity-Temperature-Depth sensors (Sea Bird CTD, model SBE-9) and eleven Niskin bottles with Teflon covered springs, was used at every station to acquire continuous data of the upper water column characteristics from the surface down to 750 m depth or to within 10 m of the bottom at shallower stations. Water samples (35 ml) from the Niskin bottles were placed in acid-cleaned high density polyethylene bottles (50 ml) and frozen until time of analysis (during April–May of each year) at the Universidad Católica de Valparaiso, Chile. Inorganic nutrient concentrations (nitrate + nitrite, phosphate, and silicic acid) were determined in an autoanalyzer following the techniques described by Atlas et al. (1971). Throughout the text we use the term *nitrate* to indicate the concentration of nitrate plus nitrite.

During 1991 samples for nutrient analyses were obtained from 11 depths (0 to 100 m) at all stations where primary production measurements were made (total of 17). During our studies in 1992 and 1993 we took water samples for nutrient analysis from four depths (5, 50, 200, and 750 m) at every station in order to be able to contour the distribution of nutrient concentrations throughout the sampling grid.

In order to test differences in nutrient concentrations among the different regions described for the AMLR study area, a non-parametric statistical analysis, Kruskal-Wallis (Zar 1984), was used. Also, a posteriori test (Nemenyi procedure) was used whenever required by the analysis.

Results

The Temperature-Salinity (T-S) diagrams from all the stations in the sampling grid could be described by three general patterns of T-S structures (Fig. 2). The T-S diagrams in Fig. 2A are typical of Drake Passage waters, those in Fig. 2B

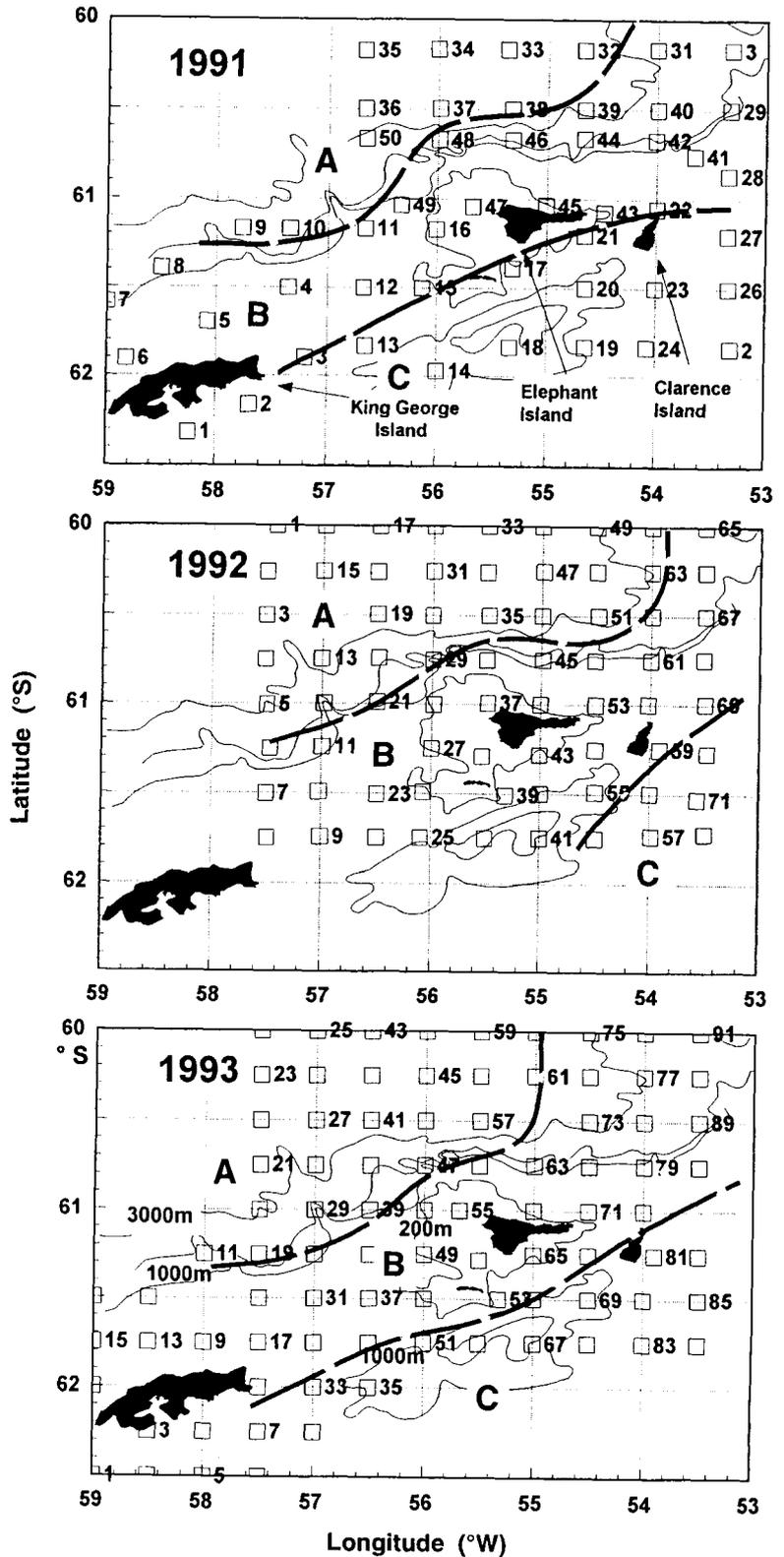


Fig. 1. Station locations within the AMLR (U.S. Antarctic Marine Living Resources Programme) sampling grid around Elephant Island, Antarctica, during 1991, 1992, and 1993. Regions A, B, and C, which are separated by thick lines, represent three different regions as judged by Temperature-Salinity characteristics in the upper 750 m of the water column (note that the demarcation lines separating these three regions vary from year to year). The thinner lines show depth contours in metres.

are typical for the transition or confluence zone between Bransfield and Drake Passage waters and those shown in Fig. 2C are typical of Bransfield Strait. The water masses involved in these T-S structures are (1) Antarctic Surface Water (AASW) which includes the Winter Water (WW) remnant, (2) the Upper and Lower Circumpolar Deep Water (UCDW and LCDW, respectively), (3) Bransfield Surface Water (BSW), and (4) Bransfield Deep Water (BDW).

The T-S diagrams shown in Fig. 2A, B, and C are representative of all stations within the regions designated as A, B, and C, respectively, as shown in Fig. 1. The T-S structure associated with region A (Fig. 2A) includes contributions from the AASW, the UCDW and the LCDW water masses. Stations in this region show a temperature minimum ($<0^{\circ}\text{C}$) between 50 to 150 m, which represents the WW of the AASW. The T-S structure associated with region C (Fig. 2C) includes BSW and the BDW, while the T-S structures associated with region B (Fig. 2B) are the result of mixing in different proportions of Drake Passage and Bransfield Strait waters. The open circles in Fig. 2B represent the T-S diagrams of stations most similar to those in Region A, while the solid squares represent the T-S diagrams of stations most similar to those in Region C.

Concentrations of nitrate, phosphate, and silicic acid in the upper 100 m of the water column of all the stations in regions A, B, and C, for which nutrient samples were obtained in 1991, are shown in Fig. 3. The major difference between the three regions is that silicic acid concentrations in region A (25 to 42 mmol m^{-3} in surface waters and 40 to 56 mmol m^{-3} at 100 m) are much lower than in regions B or C, where the corresponding values are 55 to 80 mmol m^{-3} in surface waters and 74 to 83 mmol m^{-3} at 100 m. The one station in region A with higher than average Si in surface waters was station A37, which is at or very close to the mixing front with region B; the higher Si concentrations in the upper 50 m thus probably signifies some mixing with the higher Si-containing waters of region B.

Variations in nitrate or phosphate concentrations between the three regions were much smaller than for silicic acid. In regions A and C, nitrate and phosphate concentrations are fairly uniform in the upper 50 m of the water column at stations within each zone, but both nutrients are generally slightly higher in region C than in region A. Nutrient concentrations in region B show a

greater spread, which is most likely related to the physical mixing of waters from regions A and C. Nitrate concentrations in region B segregate into two groups; the stations with lower nitrate concentrations are all geographically close to region A, while the three stations with the higher nitrate levels are located in proximity to region C.

The concentrations of nitrate, phosphate, and silicic acid at 5 m and 200 m at all stations in the sampling grid in 1992 and 1993 are shown by the contoured data in Figs. 4, 5, and 6, respectively. There is considerable mesoscale patchiness in the nitrate concentrations in surface waters (Fig. 4), with lowest concentrations in regions A and B and highest concentrations in the southeastern portion of the sampling grid within Region C. At 200 m, the situation is reversed, with the highest nitrate concentrations being found in region A. The pattern of phosphate concentrations (Fig. 5) is quite similar to that of nitrate; at 5 m depth lowest concentrations are found within region A, whereas at 200 m stations within region A generally show the highest phosphate concentrations. The pattern of distribution of silicic acid concentrations (Fig. 6) at 5 m depth is quite similar to that of either nitrate or phosphate, but the range of silicic acid concentrations between regions A and C is much greater. At 200 m, however, the lowest concentrations were also found within region A, in contrast to the pattern for either nitrate or phosphate.

At 5 m depth, stations within region A have slightly lower N and P concentrations than stations in regions B or C, but the concentrations of Si are only approximately 50 % of those in regions B or C (Table 1). At 200 m, N and P concentrations are slightly higher in region A than in regions B or C, whereas Si concentrations in region A are lower than in regions B or C. The N/P ratios at all stations at 5 m or 200 m are similar to the Redfield ratio of 16/1 (Redfield et al. 1963), while the Si/P ratios varied in Region A from 23/1 at 5 m depth to 35/1 at 200 m. However, Si/P ratios in Regions B and C were similar at both depths, ranging from 37/1 to 44/1. The mean concentrations of nitrate, phosphate, and silicic acid at 5 m depth during each leg for the years of 1991 to 1993, together with results of the statistical test to indicate any significant differences between mean nutrient values, are shown in Table 1. The internal variability within each region during the three years was such that there was a significant difference ($P < 0.01$) in

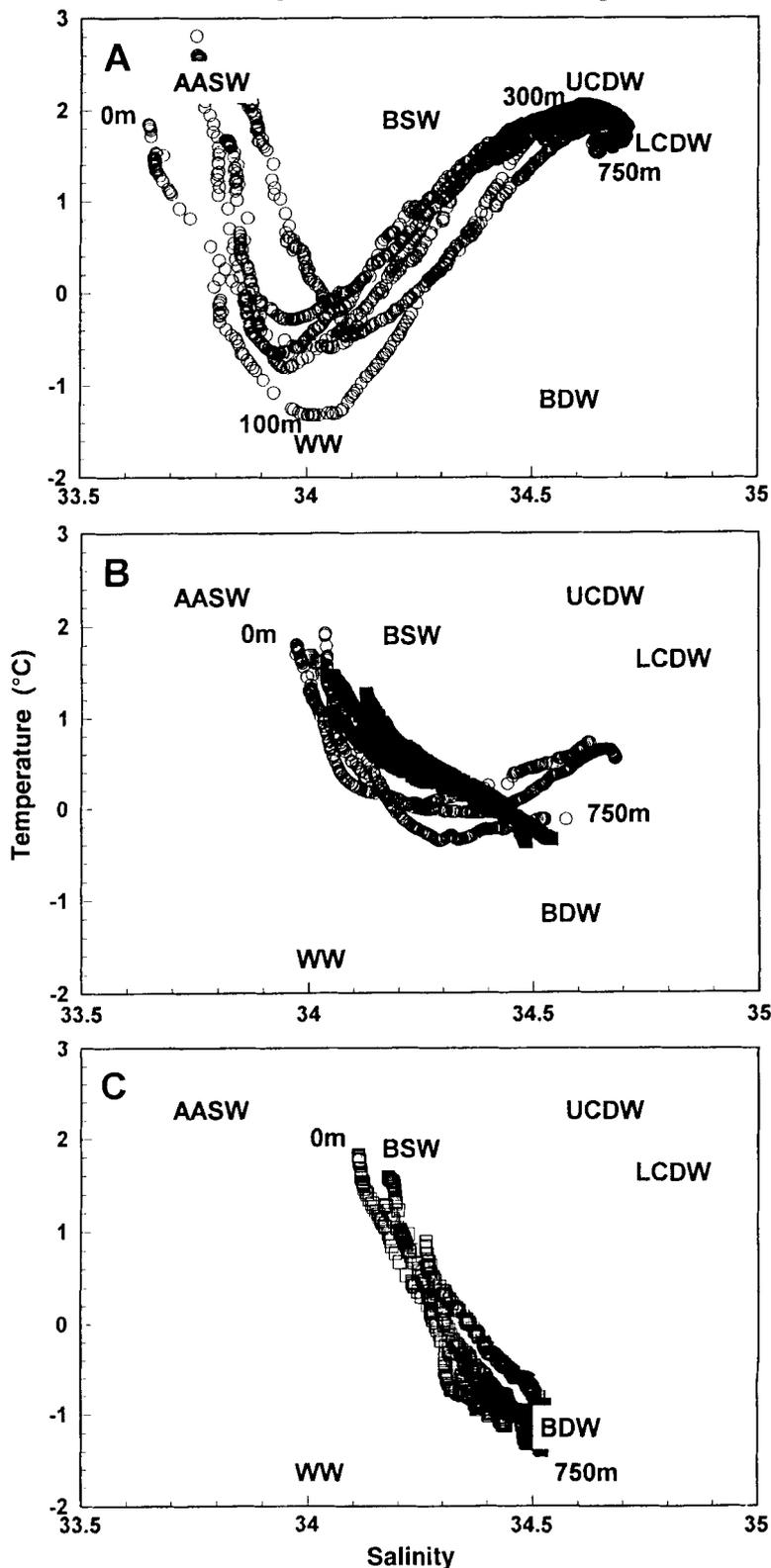


Fig. 2. Temperature-Salinity diagrams for the three major regions present in the AMLR (U.S. Antarctic Marine Living Resources Programme) sampling grid around Elephant Island. Water masses: AASW, Antarctic Surface Water; WW, Winter Water; BSW, Bransfield Surface Water; BDW, Bransfield Deep Water; UCDW, Upper Circumpolar Deep Water; LCDW, Lower Circumpolar Deep Water. The approximate location in the T-S diagram of the water masses present in the entire AMLR sampling grid are reproduced in A, B, and C, for comparison purposes, even if they are not present in that region. A, composite diagram for six representative stations in region A; B, six representative stations in region B showing the variations in T-S structure within this region; (○) are for stations relatively close to region A, and (●) are for stations close to region C; C, six representative stations in region C.

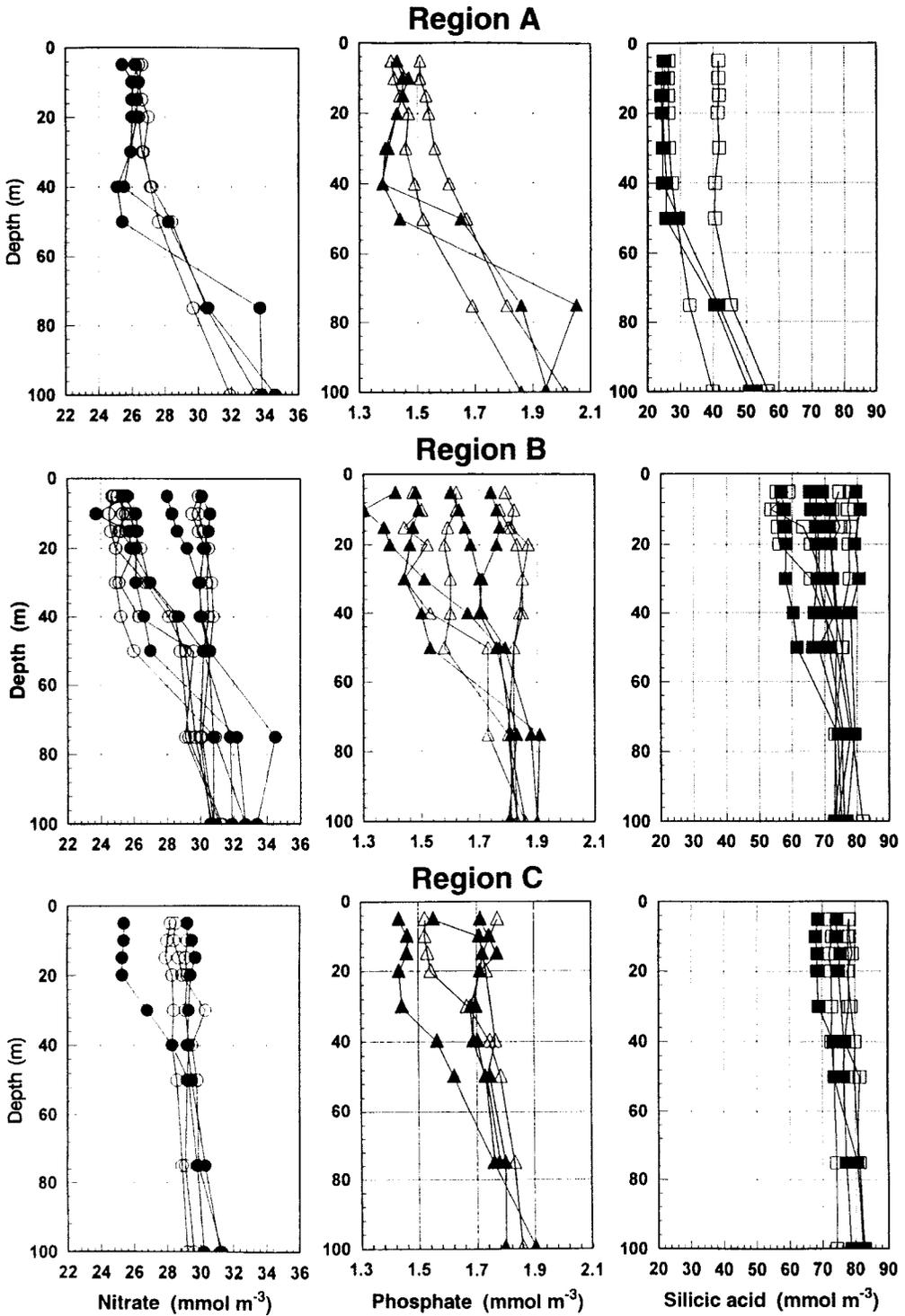


Fig. 3. Concentrations of nitrate, phosphate, and silicic acid in the upper 100 m of the water column in January to March of 1991 for representative stations in regions A, B, and C. Open symbols indicate samples collected during Leg I and solid symbols indicate samples during Leg II.

Table 1. Mean inorganic nutrient concentrations (mmol m^{-3}) for nitrogen (N), phosphate (P) and silicic acid (Si) for Leg I (I) and Leg II (II) for the years 1991, 1992 and 1993; statistical analysis to test differences in nutrient concentrations for samples at 5 m within regions A, B, and C of the AMLR sampling grid, and Si/N/P ratios at 5 m and 200 m. The lines under the years and Legs indicate groups of data that were not significantly different.

Cruise	Region A (5m)			Region B (5m)			Region C (5m)		
	N	P	Si	N	P	Si	N	P	Si
I - 91	26.5	1.46	34.5	27.0	1.85	65.6	27.7	1.76	76.3
II - 91	25.8	1.43	25.0	26.8	1.73	66.0	27.4	1.56	73.0
I - 92	27.5	1.72	39.7	28.1	1.84	66.4	29.8	2.0	80.0
II - 92	27.8	1.82	52.0	29.3	1.94	72.2	29.9	2.02	84.4
I - 93	26.2	1.72	32.8	26.3	1.79	68.8	27.8	1.88	89.9
II - 93	25.2	1.67	41.7	26.9	1.83	32.7	27.6	1.89	90.3

Statistical analysis for samples at 5m depth

N	<u>II3</u> <u>II1</u> <u>I3</u> <u>I1</u> <u>I2</u> <u>II2</u>	<u>I3</u> <u>II3</u> <u>II1</u> <u>I1</u> <u>I2</u> <u>II2</u>	<u>II1</u> <u>I1</u> <u>I3</u> <u>I3</u> <u>I2</u> <u>II2</u>
	P<0.01	P<0.01	P<0.01
P	<u>II1</u> <u>I1</u> <u>II3</u> <u>I2</u> <u>I3</u> <u>II2</u>	<u>II1</u> <u>I1</u> <u>I3</u> <u>II3</u> <u>I2</u> <u>II2</u>	<u>II1</u> <u>I1</u> <u>I3</u> <u>II3</u> <u>I2</u> <u>II2</u>
	P<0.01	P<0.01	P<0.01
Si	<u>II1</u> <u>I3</u> <u>II</u> <u>I2</u> <u>II3</u> <u>II2</u>		<u>II1</u> <u>I1</u> <u>I2</u> <u>II2</u> <u>I3</u> <u>II3</u>
	P<0.01	P=0.05	P<0.01

Mean concentrations and Si/N/P ratios

5m depth									
Mean	26.5	1.64	37.6	27.4	1.84	68.9	28.3	1.85	82.3
Si/N/P	23/16/1			37/15/1			44/15/1		
200m depth									
Mean	34.3	2.31	80.3	32.5	2.20	89.3	31.6	2.16	91.9
Si/N/P	35/15/1			41/15/1			43/15/1		

nutrient concentrations at 5 m depth for nitrogen, phosphorus and silicic acid with the exception of silicic acid in region B where the probability was equal to 0.05 (Table 1). In general, 1992 was the year with higher nitrate and phosphate concentrations and 1991 was the year with the lowest concentrations in the three regions, with minor exceptions.

Data in Table 2 show the seasonal depletion of N, P, and Si in the upper 100 m in each region

during January to March of 1991, assuming that the values at 100 m represent the concentrations in surface waters at the end of winter. It is seen that the greatest depletion is found in region A, and the least in region C. The ratios of depletion of Si and N relative to P also varies between the regions, with stations in region A having the largest Si/P and N/P depletion ratios (50/1 and 16/1, respectively) and region C the smallest ratios (17/1 and 6/1, respectively).

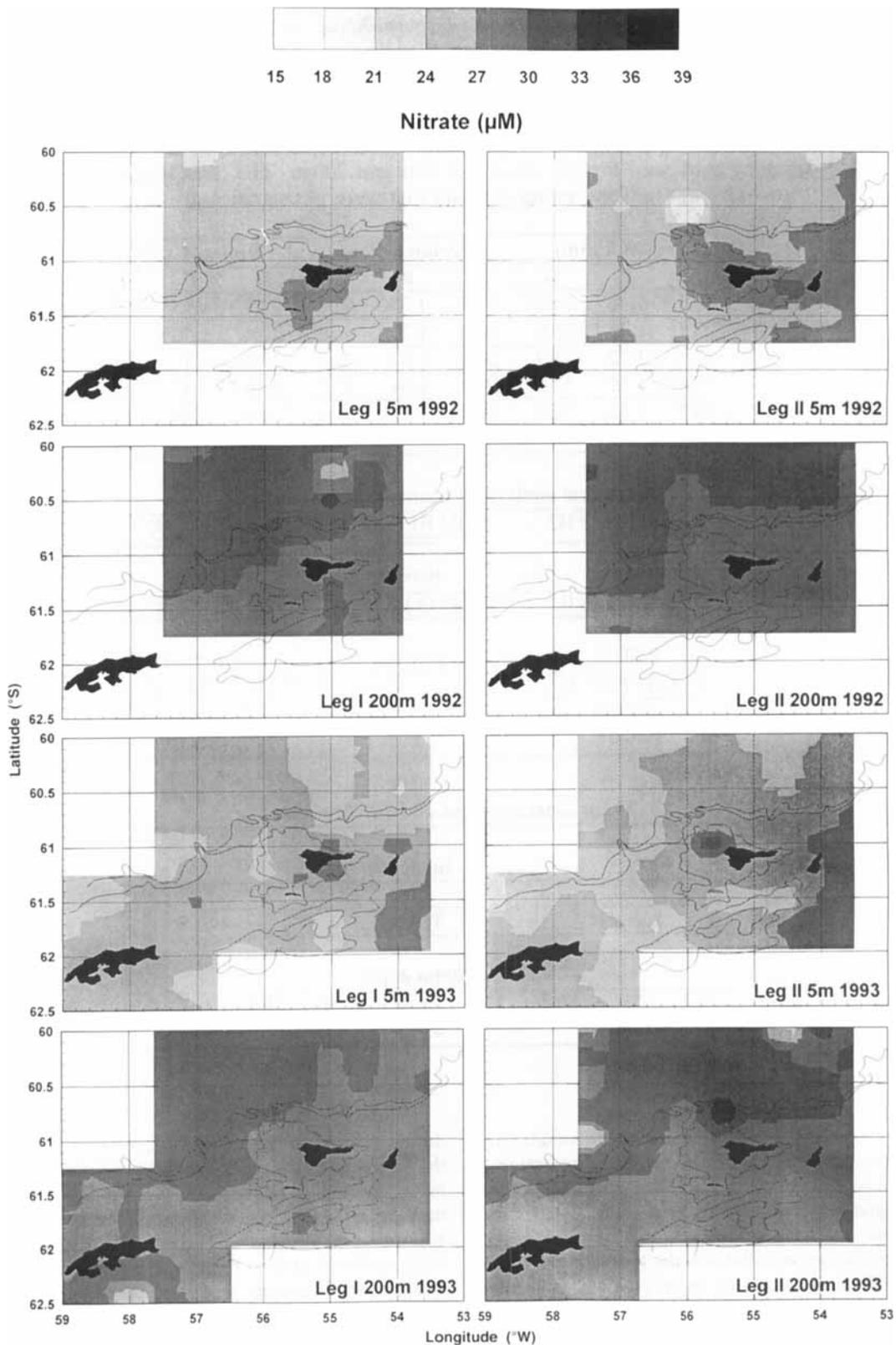
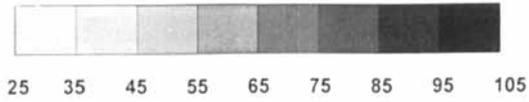


Fig. 4 Contour maps of nitrate concentrations at 5 m and 200 m during Leg I and Leg II of 1992 and 1993.



Silicic acid (μM)

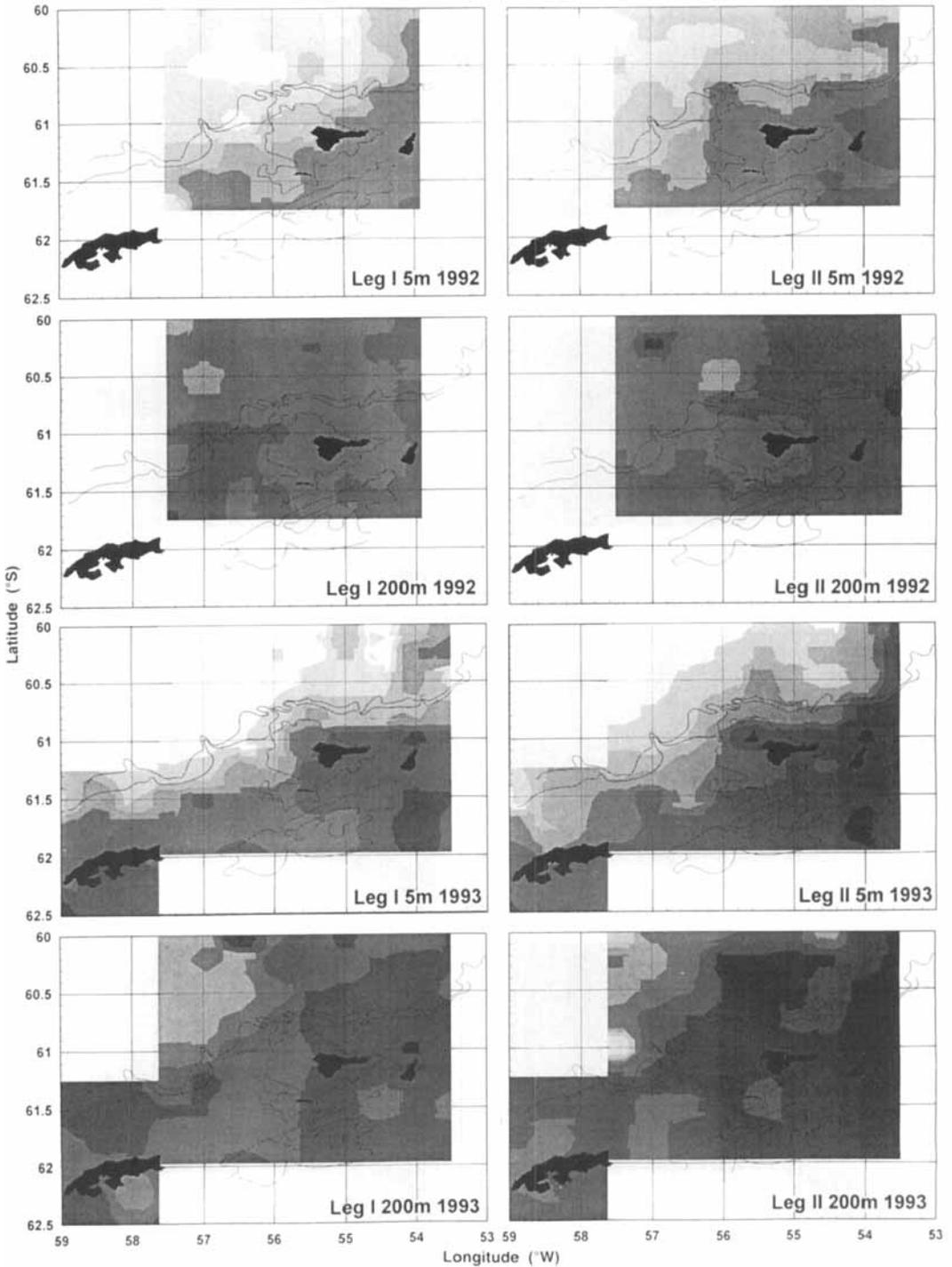


Fig. 5. Contour maps of phosphate concentrations at 5 m and 200 m during Leg I and Leg II of 1992 and 1993.

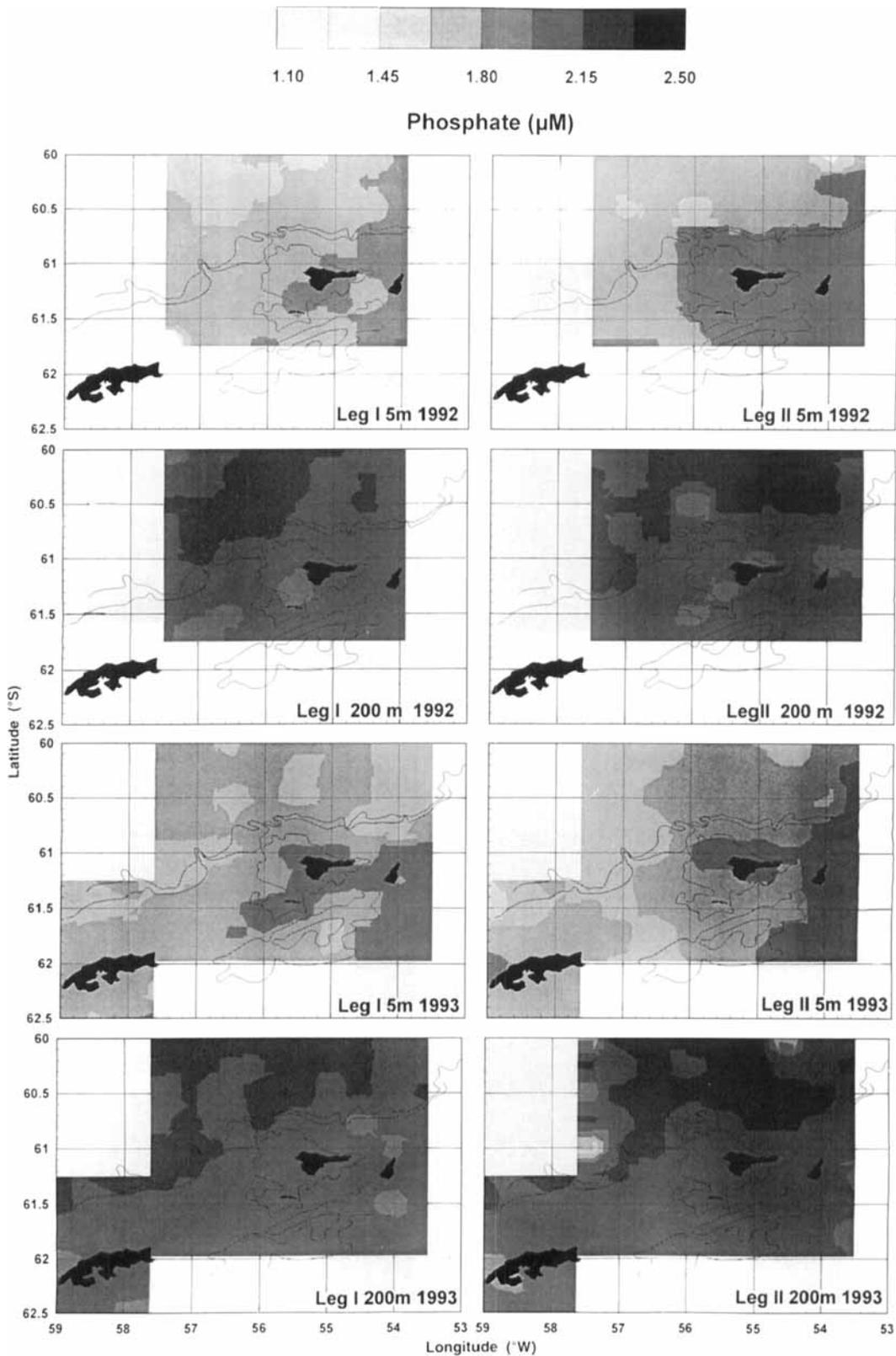


Fig. 6. Contour maps of silicic acid concentrations at 5 m and 200 m during Leg I and Leg II of 1992 and 1993.

Table 2. Calculated nutrient deficits (mmol m^{-2} , 0 to 100 m) within regions A, B and C, and ratios of the deficits. Data are from 1991

	Region A	Region B	Region C
Nitrogen (N)	488	215	116
Phosphorus (P)	30.3	17.9	20.3
Silicic acid (Si)	1509	449	338
Si/N/P	50/16/1	25/12/1	17/6/1

Discussion

Our physical data (see Fig. 2) indicate that most of the stations in the AMLR grid are located in AASW (Region A in Fig. 1) and in the wide mixing zone between AASW from the Drake Passage and Bransfield Strait waters (Region B). The T-S structures for stations in region C (Fig. 2C) represent mostly Bransfield Strait waters. Nevertheless, there is a possibility of some influence of water from the Weddell Sea or from the Weddell-Scotia Confluence (WSC) to the south-east of Elephant Island.

Inorganic nutrients were relatively high throughout the entire sampling grid (Figs. 4, 5, and 6). All stations in region A, however, could be distinguished from those in regions B and C by significantly lower concentrations of silicic acid in the upper 100 m (Fig. 3), resulting in lower Si/P ratios (Table 1). Although we have grouped stations in region B and considered it as a transition zone between regions A and C, there is considerable variability in T-S diagrams (Fig. 2) and in nutrient concentrations (Fig. 3, 4, 5, 6, and Table 1) in this region. This undoubtedly results from different nutrient conditions and mixing between regions A and C. As the concentrations of N, P and Si in all regions are well above published K_s constants for these nutrients (Eppley et al. 1969; Perry & Eppley 1981; Nelson & Tréguer 1992), it is unlikely that concentrations of these nutrients are limiting phytoplankton growth anywhere within the AMLR study area. This conclusion does not exclude the possibility of growth limitation by micronutrients (e.g., Fe) as suggested by Martin et al. (1990) and given considerable credence by experiments with addition of Fe to sea water samples (de Baar et al. 1990; Helbling et al. 1991).

In order to understand the variability of nutrient concentrations it is necessary to know the

distribution and productivity of phytoplankton in the area as well as the autotrophic/heterotrophic characteristics of the food web. Our data indicate that there were relatively small changes in inorganic nutrient concentrations between Leg I and Leg II of each year, in spite of the fact that the month between each Leg occurs during the austral summer period (Jan–Feb). The measured rates of primary production in regions A, B, and C during this period averaged 225, 450, and 380 $\text{mg C m}^{-2} \text{day}^{-1}$ (Helbling et al. 1995), which would equate to assimilation of approximately 0.03 to 0.06 $\mu\text{mol N l}^{-1} \text{day}^{-1}$ throughout the euphotic zone. These nitrogen assimilation numbers are comparable to the ones reported by Rönner et al. (1983) in a nearby area of the Scotia Sea. If these rates are valid for the entire month between the two Legs the decrease in nutrient concentrations should have been detected by our nutrient analyses, unless rates of upwelling and/or regeneration of nutrients were high. The data in Table 2, however, show that there are significant nutrient deficits in the euphotic zone for all three nutrients in all three regions when comparing winter to summer nutrient concentrations, in spite of the fact that there were only relatively small differences between the two Legs (Table 1). These data are in agreement with seasonal studies of rates of regeneration, which show high rates of ammonium assimilation relative to nitrate uptake in summer (Rönner et al. 1983) and significantly lower relative ammonium assimilation rates in fall or spring (Koike et al. 1986).

The calculated nutrient deficits in the upper 100 m showed considerable differences between the three regions (Table 2). Greatest depletion was found in region A for all three nutrients, with the least depletion being in region C except for P depletion, which was lowest in region B. Region A, however, also had the lowest rate of primary production as noted above. It is interesting to

note that these seasonal deficits do not correlate very well with the measured rate of primary production in the three regions as region A has the lowest rate of primary production but showed the greatest nutrient deficits. We believe that the reasons for this lack of agreement between primary production and nutrient deficits include the following processes:

(1) Historical data (Gordon & Molinelli 1982; Sommer & Stabel 1986) show that concentrations of both N and P, and particularly Si, decrease progressively from Elephant Island to the north and northwest. Waters coming from the Bellingshausen Sea, as well as from Bransfield Strait, generally do not show as steep a gradient in nutrient concentrations as they have more recently been ice-covered and thus have had a shorter period for phytoplankton growth compared to Drake Passage waters (Nelson et al. 1987). The marked loss of Si from Drake Passage waters is most likely due to the refractory nature of Si in diatom frustules, which results in Si-rich sedimentation to the benthos (Le Jehan & Tréguer 1983; Tréguer et al. 1989). In shallower waters over the continental shelf (most of regions B and C), there is likely to be considerable mineralisation in the sediments and subsequent enrichment of the water column with N, P and Si by physical mixing processes.

(2) Stations in regions B and C apparently experience a greater rate of nutrient input due to an upwelling of Circumpolar Deep Water (Sievers & Nowlin 1984) which is rich in nutrients, together with the possibility of continuous injection of nutrients into the euphotic zone by turbulent mixing processes. Such injection of nutrients in these two regions will decrease the apparent nutrient deficits in the upper water column. This would be in agreement with the north-south nutrient sections shown by Sievers & Nowlin (1984) and with the Si/P ratios shown in Table 1. As shown by Holm-Hansen et al. (1994), the stability of the water column, as indicated by the vertical gradient in Sigma-t, decreased from region A to region C.

(3) Biological regeneration processes in the euphotic zone will also diminish the magnitude of the apparent nutrient deficit. It is known that there is much regeneration of nutrients in these waters (Rönner et al. 1983; Koike et al. 1986), so it is not surprising that significant changes in nutrient concentrations were not detected during the two-month period of each AMLR cruise. The fact that significant nutrient deficits do develop

between late winter and early summer most likely reflects the autotrophic nature of the planktonic communities during spring time, which would be consistent with low rates of nutrient regeneration and primary production being based primarily on assimilation of nitrate (Tréguer & Jacques 1992).

Using the measured rates of production during the AMLR cruises, the length of time required to generate the observed nutrient deficits in regions A, B and C would be approximately 180, 40 and 25 days, respectively; this would indicate that higher production rates must prevail in region A during the spring. Regional differences in the depth of the upper mixed layer (UML) did not affect the above depletion rates to any significant extent as the UML averaged between 44–50 m throughout the sampling area, and the depth of the euphotic zone was close to 90 m depth (Helbling et al. 1995).

Results from the statistical analyses showed that in general the year of 1991 tended to have lower nutrient concentrations as compared to 1992 and 1993 (Table 1). This is consistent with phytoplankton biomass data (Helbling et al. 1995) as phytoplankton concentrations, integrated throughout the euphotic zone, during 1991 were about double the concentrations observed during 1992 and 1993 in the three regions. The phytoplankton crop in Region A was usually dominated by nanoplanktonic diatoms such as *Fragilariopsis pseudonana*; while Region B, although it tended to be dominated by microplanktonic diatoms such as *Pseudonitzschia* spp, *Proboscia alata* and *Rhizosolenia antennata* f. *semispina* (Villafañe et al. 1993), often contained significant numbers of cryptophytes and flagellates (Villafañe et al. in press). However, the phytoplankton in Region C was dominated by cryptophytes and flagellates ranging from 2 to 10 μm (Villafañe 1993). These differences in dominance of species could explain part of the variability observed in nutrient uptake ratios, as areas dominated by diatoms (regions A and B) showed more Si uptake (Table 2) than in region C which was dominated by flagellates. Region C also showed a low ratio N/P uptake (6/1) as compared to regions A and B where the ratios were 16/1 and 12/1, respectively. One possible explanation of the low N/P uptake ratio in region C is that production of ammonia (i.e., via zooplankton grazing and excretion) could play an important role in decreasing nitrate assimilation rates. In addition to high concentrations of Antarctic krill (*Euphausia superba*) in this area (Hew-

itt & Demer 1993), region C also had maximum concentrations of salps (*Salpa thomsoni*) and the euphausiid *Thysanoessa macrura* (Loeb et al. 1992, 1993b; Park & Wormuth 1993).

The results discussed in this paper, coupled with other data in the literature, point out the possible inherent errors if one attempts to estimate daily or seasonal production in Antarctic waters based on nutrient deficits in the upper water column. The reliability of such estimates will be related to both physical and biological factors. The biological factors include (1) variability in the winter-time concentrations of nutrients (e.g., the low Si concentrations in Drake Passage waters in contrast to Weddell Sea waters); (2) chemical composition of the phytoplankton crop, which will depend upon what phylogenetic groups are dominant (e.g., diatoms or silicoflagellates with high Si content, in contrast to cryptophytes or flagellates); (3) the size and sinking rates of the dominant phytoplankton species; (4) the rate of regeneration of nutrients in the upper water column, which will be dependent upon the nature of the heterotrophic assemblages (especially the bacterioplankton, microzooplankton, and macro-zooplankton); and (5) the seasonality in phytoplankton species succession and variations in the ratio of autotrophic to heterotrophic biomass. Primary production estimates based on such nutrient deficits will represent minimal values. The error will probably be less if working within one well-defined water mass such as the Weddell Sea (e.g. Jennings et al. 1984) as compared to an oceanographically complex area as the AMLR sampling grid around Elephant Island. Our data from the AMLR programme illustrate the great biological and chemical variability occurring within one fairly small geographical region, and point out the necessity of a multidisciplinary programme in order to understand the seasonal changes in primary production in Antarctic waters.

Acknowledgements. – Shipboard studies related to this research were supported by National Oceanic and Atmospheric Administration (NOAA) through the U.S. Antarctic Marine Living Resources Programme (AMLR, grants to O. Holm-Hansen). All nutrient analyses were supported in part by Universidad Católica de Valparaíso, Valparaíso, Chile. We thank the officers and crew of NOAA ship *SURVEYOR* for their support in all aspects of the field work, and Chief Scientists R. Holt and R. Hewitt for their work and support which made this project possible. Grateful acknowledgment is also made to all the people who worked in our group during cruises. We thank Maria Angelica Varas S., Noe Caceres L., and Jorge Osorio E.

for their assistance with the chemical analyses, two anonymous reviewers for their helpful comments and O. Holm-Hansen III for graphics consultation.

References

- Amos, A. F. 1984: Distribution of krill (*Euphausia superba*) and the hydrography of the Southern Ocean: Large-scale processes. *J. Crust. Biol.* 4(1), 306–329.
- Atlas, E. L., Gordon, L. I., Hager, S. W. & Park, P. K. 1971: A practical manual for the use of the Technicon Autoanalyzer in seawater nutrient analyses: Revised. Oregon State University, Department of Oceanography. Technical Report 71–22. 49 pp.
- Brinton, E., Loeb, V. J., Macaulay, M. C. & Shulenberger E. 1987: Variability of *Euphausia superba* populations near Elephant Island and the South Shetlands: 1981 vs. 1984. *Polar Biol.* 7, 345–362.
- Burkholder, P. R. & Sieburth, J. M. 1961: Phytoplankton and chlorophyll in the Gerlache and Bransfield Straits of Antarctica. *Limnol. Oceanogr.* 6, 45–52.
- Clowes, A. I. J. 1934: Hydrology of the Bransfield Strait. *Discovery Rep.* IX, 1–64.
- de Baar, H. J. W., Buma, A. G. J., Nolting, R. F., Cadec, D. C., Jacques, G. & Tréguer, P. J. 1990: On iron limitation of the Southern Ocean: experimental observation in the Weddell and Scotia Seas. *Mar. Ecol. Prog. Ser.* 65, 105–122.
- El-Sayed, S. Z. 1970: On the Productivity of the Southern Ocean. Pp. 119–135 in Holdgate, M. W. (ed.): *Antarctic Ecology*. Academic Press, London.
- Eppley, R. W., Rogers, J. N. & McCarthy, J. J. 1969: Half-saturation constants for uptake of nitrate and ammonium by marine phytoplankton. *Limnol. Oceanogr.* 14, 912–920.
- Gordon, A. L. 1988: Spatial and temporal variability within the Southern Ocean. Pp. 41–56 in Sahrhage, D. (ed.): *Antarctic Ocean and Resources Variability*. Springer Verlag, Berlin.
- Gordon, A. L. & Nowlin, W. D. 1978: The basin waters of the Bransfield Strait. *J. Phys. Oceanogr.* 8, 258–264.
- Gordon, A. L. & Molinelli, E. M. 1982: Southern Ocean Atlas: Thermohaline Chemical Distributions and the Atlas Data Set. Columbia University Press, New York.
- Helbling, E. W., Villafane V. & Holm-Hansen O. 1991: Effect of Fe on productivity and size distribution of Antarctic phytoplankton. *Limnol Oceanogr.* 36 (8), 1879–1885.
- Helbling, E. W., Amos, A. F., Silva S., N., Villafañe, V. & Holm-Hansen, O. 1993: Phytoplankton distribution and abundance as related to a frontal system north of Elephant Island, Antarctica. *Antarctic Sci.* 5 (1), 25–36.
- Helbling, E. W., Villafañe, V. & Holm-Hansen, O. 1995: Variability of phytoplankton distribution and primary production around Elephant Island, Antarctica, during 1990–1993. *Polar Biol.* 15, 233–246.
- Hewitt, R. P. & Demer, D. A. 1993: Dispersion and abundance of Antarctic krill in the vicinity of Elephant Island in the 1992 austral summer. *Mar. Ecol. Prog. Ser.* 99, 29–39.
- Holm-Hansen, O. & Mitchell, B. G. 1991: Spatial and temporal distribution of phytoplankton and primary production in the western Bransfield Strait region. *Deep-Sea Res.* 38 (8/9), 961–980.
- Holm-Hansen, O., Amos, A. F., Silva S., N., Villafañe, V. & Helbling, E. W. 1994: *In situ* evidence for a nutrient limitation of phytoplankton growth in pelagic Antarctic waters. *Antarctic Sci.* 6(3), 315–324.

- Jacobs, S. S. 1991: On the nature and significance of the Antarctic slope front. *Mar. Chem.* 35, 9–24.
- Jennings, J. C., Gordon, L. I. & Nelson, D. M. 1984: Nutrient depletion indicates high primary productivity in the Weddell Sea. *Nature*, 309, 51–54.
- Kamykowski, D. & Zentara, S. J. 1989: Circumpolar plant nutrient covariation in the Southern Ocean: patterns and processes. *Mar. Ecol. Prog. Ser.* 58(1), 101–111.
- Koike, I., Holm-Hansen, O. & Biggs, D. C. 1986: Inorganic nitrogen metabolism by Antarctic phytoplankton with special reference to ammonium cycling. *Mar. Ecol. Prog. Ser.* 30, 105–116.
- Le Jehan, S. & Tréguer, P. 1983: Uptake and regeneration $\Delta Si/\Delta N/\Delta P$ ratios in the Indian sector of the Southern Ocean. Originality of the biological cycle of silicon. *Polar Biol.* 2, 127–136.
- Le Jehan, S. & Tréguer, P. 1985: The distribution of inorganic nitrogen, phosphorus and dissolved organic matter in surface and deep waters of the Southern Ocean. Pp. 22–29 in Siegfried, W. R., Condy, P. R. & Laws, R. M. (eds.): *Antarctic Nutrient Cycles and Food Webs*. Springer-Verlag, Berlin.
- Loeb, V., Davis, K., Roddy, F., Siegel, V. & Kelly, D. 1992: Direct krill and zooplankton sampling. Pp. 51–66 in Rosenberg, J. & Hewitt, R. (eds.): *AMLR 1991/92 field season report*. Report LJ-92-17.
- Loeb, V. J., Amos, A. F., Macaulay, M. C. & Wormuth, J. H. 1993a: Antarctic krill stock distribution and composition in the Elephant Island and King George Island areas, January–February, 1988. *Polar Biol.* 13, 171–181.
- Loeb, V., Siegel, V., Follegati, R., Kruse, S., Laman, N., Low, D., Rodriguez, L. & Watters, G. 1993b: Direct krill and zooplankton sampling. Pp. 47–68 in Rosenberg, J. (ed.): *AMLR 1992–93 field season report*. Report LJ-93-08.
- Macaulay, M. C., English, T. S. & Mathisen, O. A. 1984: Acoustic characterization of swarms of Antarctic krill (*Euphausia superba*) from Elephant Island and Bransfield Strait. *J. Crust. Biol.* 4(1), 16–44.
- Martin, J. H., Gordon, R. M. & Fitzwater, S. E. 1990: Iron in Antarctic waters. *Nature* 345, 156–158.
- Nast, F., Kock, K. H., Sahrhage, D., Stein, M. & Tiedtke, J. E. 1988: Hydrography, krill and fish and their possible relationships around Elephant Island. Pp. 183–198 in Sahrhage, D. (ed.): *Antarctic Ocean and Resources Variability*. Springer-Verlag, Berlin.
- Nelson, D. M. & Smith, W. O. 1986: Phytoplankton bloom dynamics of the Ross Sea ice edge. II. Mesoscale cycling of nitrogen and silicon. *Deep-Sea Res.* 33, 1389–1412.
- Nelson, D. M. & Tréguer, P. 1992: Role of silicon as a limiting nutrient to Antarctic diatoms: evidence from kinetic studies in the Ross Sea ice-edge zone. *Mar. Ecol. Prog. Ser.* 80, 255–264.
- Nelson, D. M., Smith, W. O., Gordon, L. I. & Huber, B. A. 1987: Spring distributions of density, nutrients, and phytoplankton biomass in the ice edge zone of the Weddell-Scotia Sea. *J. Geophys. Res.* 92 (7), 7181–7190.
- Neori, A. & Holm-Hansen, O. 1982: Effect of temperature on rate of photosynthesis in Antarctic phytoplankton. *Polar Biol.* 1, 33–38.
- Park, C. & Wolmuth, J. H. 1993: Distribution of Antarctic zooplankton around Elephant Island during the austral summers of 1988, 1989, and 1990. *Polar Biol.* 13, 215–225.
- Patterson, S. L. & Sievers, H. A. 1980: The Weddell-Scotia Confluence. *J. Phys. Oceanogr.* 10, 1584–1610.
- Perry, M. J. & Eppley, R. W. 1981: Phosphate uptake by phytoplankton in the central North Pacific Ocean. *Deep-Sea Res.* 28, 39–49.
- Redfield, A. C., Ketchum, B. H., & Richards, F. A. 1963: The influence of organisms on the composition of sea-water. Pp. 26–77 in Hill, M. N. (ed.): *The Sea, Vol. 2*. J. Wiley, New York, London.
- Rönner, U., Sörensson, F. & Holm-Hansen, O. 1983: Nitrogen assimilation by phytoplankton in the Scotia Sea. *Polar Biol.* 2, 137–147.
- Sievers, H. A. 1982: Descripción de las condiciones oceanográficas físicas, como apoyo al estudio de la distribución y comportamiento del krill. *INACH. Ser. Cient.* 28, 87–136.
- Sievers, H. A. & Nowlin, W. D. 1984: The stratification and water masses at Drake Passage. *J. Geophys. Res.* 89 (C6), 10489–10514.
- Sievers, H. A. & Nowlin, W. D. 1988: Upper ocean characteristics in Drake Passage and adjoining areas of the Southern Ocean. 39°W–95°W. Pp. 57–80 in Sahrhage, D. (ed.): *Antarctic Ocean and Resources Variability*. Springer-Verlag, Berlin.
- Silva S., N. 1985: Chemical oceanography of the Bransfield Strait: micronutrient compounds SIBEX Cruise-Phase I Chile. *INACH Ser. Cient.* 33, 47–81.
- Silva S., N. 1986: Chemical oceanography of the Bransfield Strait: micronutrient compounds (SIBEX-Phase II Cruise, Chile) *INACH Ser. Cient.* 35, 7–37.
- Sommer, U. & Stabel, H. H. 1986: Near surface nutrient and phytoplankton distribution in the Drake Passage during early December. *Polar Biol.* 6, 107–110.
- Stein, M. 1988: Variation of geostrophic circulation off the Antarctic Peninsula and in the Southwest Scotia Sea, 1975–1985. Pp. 81–91 in Sahrhage, D. (ed.): *Antarctic Ocean and Resources Variability*. Springer-Verlag, Berlin.
- Sverdrup, H. U. 1933: On vertical circulation in the ocean due to the action of the wind with application to conditions within the Antarctic circumpolar current. *Discovery Reports VII*, 139–170.
- Tilzer, M. M. & Dubinsky, Z. 1987: Effects of temperature and day length on the mass balance of Antarctic phytoplankton. *Polar Biol.* 7, 35–42.
- Tréguer, P. & Jacques, G. 1992: Dynamics of nutrients and phytoplankton, and fluxes of carbon, nitrogen and silicon in the Antarctic Ocean. *Polar Biol.* 12, 149–162.
- Tréguer, P., Kamatani, A., Gueneley, S. & Queguiner, B. 1989: Kinetics of dissolution of Antarctic diatom frustules and the biogeochemical cycle of silicon in the Southern Ocean. *Polar Biol.* 9, 397–403.
- Villafañe, V. E. 1993: Patterns of distribution of phytoplankton species and biomass in the vicinity of Elephant Island, Antarctica, during summer 1990–92. MSc. Thesis. *Scripps Institution of Oceanography*, University of California, San Diego, 107 pp.
- Villafañe, V., Helbling, E. W. & Holm-Hansen, O. 1993: Phytoplankton around Elephant Island, Antarctica: Distribution, biomass and composition. *Polar Biol.* 13, 183–191.
- Villafañe, V., Helbling, E. W. & Holm-Hansen, O. in press: Spatial and temporal variability of phytoplankton biomass and taxonomic composition around Elephant Island, Antarctica, during summers of 1990–1993. *Mar. Biol.*
- Zar, J. H. 1984: *Biostatistical Analysis*. Prentice Hall, Inc. New Jersey, 2nd ed. 718 pp.
- Zentara, S. J. & Kamykowski, D. 1981: Geographic variations in the relationship between silicic acid and nitrate in the South Pacific Ocean. *Deep-Sea Res.* 28 (5A), 455–465.