

Whole season net community production in the Weddell Sea

Mario Hoppema · Rob Middag · Hein J. W. de Baar ·
Eberhard Fahrbach · Evaline M. van Weerlee ·
Helmuth Thomas

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Abstract Depletions of total CO₂, nitrate, phosphate and silicate in the surface layer were calculated for cruise ANT XXII/3 with FS Polarstern in March 2005 for estimating the annual net community production. East-west across the Weddell Sea the variation of all depletions is similar, but this holds to a lesser extent for silicate. Depletions in March 2005 are 2–3 times larger than those in January 1993 for the same transect. Very low N:P and C:P depletion ratios seem to point to dominance of diatoms, in the central Weddell Sea more than in the margin. Estimates of annual net community productions are about 1.8 and 3.5 mol C m⁻² year⁻¹ for the interior Weddell Sea and a near-margin region, respectively. The region does not comply with the classical view of a marginal ice zone with high productivity. Net community production is similar to annual export production, implying that remineralization in the ensuing winter be minor.

Introduction

The global carbon cycle is characterized by large variability, in which the seasonality of biological processes plays a major role. For the Southern Ocean this holds true to an even larger extent because of an additional environmental factor: ice coverage, which tends to reinforce spatial and temporal variability of biological processes and air-sea gas exchange. Autotrophic phytoplankton stands at the basis of the carbon cycle with their fixation of carbon dioxide (CO₂) from surface water. Via phytoplankton, CO₂ is transferred to other compartments of the ecosystem. Besides that, phytoplankton is a conduit for carbon transfer down the water column, where dead planktonic material is remineralized to CO₂. Within the ocean interior, this CO₂ is cut off from contact with the atmosphere for a long time. On the other hand, in the surface water CO₂ fixation by phytoplankton causes undersaturation of CO₂, which in turn drives CO₂ uptake from the atmosphere. This is the concept of the (natural) biological carbon pump. The carbon pump is subject to the variability inherent to the Southern Ocean, which complicates the reliable assessment of the uptake of atmospheric CO₂. Finally, anthropogenic activity may have impact on the carbon pump in diverse ways, e.g. changes in the stratification and mixed layer depth, changes in the supply of nutrients, or ecosystem changes.

Different approaches exist for estimating the CO₂ draw-down initiated by phytoplankton photosynthesis. Using incubation techniques, the uptake of labeled bicarbonate may be measured in water sampled in the area of investigation (Steeman Nielsen 1951). For obtaining an annual estimate of CO₂ uptake, sampling must be carried out at least several times a year and inter- or extrapolation must be performed. If the seasonal cycle is not well known, the peak productivity could be missed, and thus the method

M. Hoppema (✉) · E. Fahrbach
Alfred Wegener Institute for Polar and Marine Research,
Climate Sciences, Postfach 120161,
27515 Bremerhaven, Germany
e-mail: Mario.Hoppema@awi.de

R. Middag · H. J. W. de Baar · E. M. van Weerlee · H. Thomas
Royal Netherlands Institute for Sea Research,
Postbus 59, 1790 AB Texel, The Netherlands

R. Middag · H. J. W. de Baar
Department of Marine Biology, University of Groningen,
Postbus 14, 9750 AA Haren, The Netherlands

H. Thomas
Department of Oceanography, Dalhousie University,
Canada Research Chair, 1355 Oxford Street,
Halifax, NS, Canada, B3H 4J1

has serious restrictions. Another method is based on satellite imagery, where a primary production algorithm is applied to phytoplankton pigment concentrations (e.g., Arrigo et al. 1998). An advantage of this approach is that information is gathered from large regions where complete seasonal coverage can be achieved. However, since the satellite only detects the upper few meters of the surface layer, but productivity occurs deeper as well, there remains much uncertainty. Furthermore, a conversion of phytoplankton pigment to biomass is required. Finally, the biological consumption of CO₂ and nutrients may be estimated from surface layer deficits/depletions as compared to winter water concentrations (Le Corre and Minas 1983; Jennings et al. 1984). The latter may be determined either through genuine winter measurements, or from a remnant winter layer below the seasonal pycnocline. Although there are some assumptions inherent to this method (see below), the advantage is that the seasonally integrated consumption can be obtained from one single cruise, provided that this is conducted in the appropriate time of the year. It is worth adding that a deficit represents the net change produced by the whole community, i.e., both autotrophs and heterotrophs (see Banse 1994), and exactly this is the relevant figure for studying carbon cycle and ecosystem dynamics.

We apply the deficit method to the Weddell Sea, a region with seasonal ice coverage. If the seasonal depletions are determined towards the end of the vegetative season, approximately all seasonal CO₂ drawdown will have been captured, provided the wintertime CO₂ drawdown is negligible. Some winter observations do exist and they indeed show that the biological activity is very low (Cota et al. 1992; Scharek et al. 1994; Spiridonov et al. 1996). Here we present new CO₂ and nutrient data from the interior Weddell Sea collected near the end of the vegetative season which thus fulfill these conditions.

Materials and methods

From 22 January (Cape Town, South Africa) to 6 April 2005 (Punta Arenas, Chile), cruise ANT XXII/3 of FS Polarstern to the Southern Ocean was completed (Fahrbach 2006). In the late austral summer from 24 February to 11 March, water samples were collected across the Weddell Sea proper between Kapp Norvegia and Joinville Island at the tip of the Antarctic Peninsula (Fig. 1). Temperature and salinity profiles were obtained from the conductivity temperature depth (CTD) instrument (SBE911plus). The precision for temperature and salinity is 0.001°C and 0.002, respectively (Fahrbach 2006). Water samples were drawn from the rosette sampler coupled to the CTD.

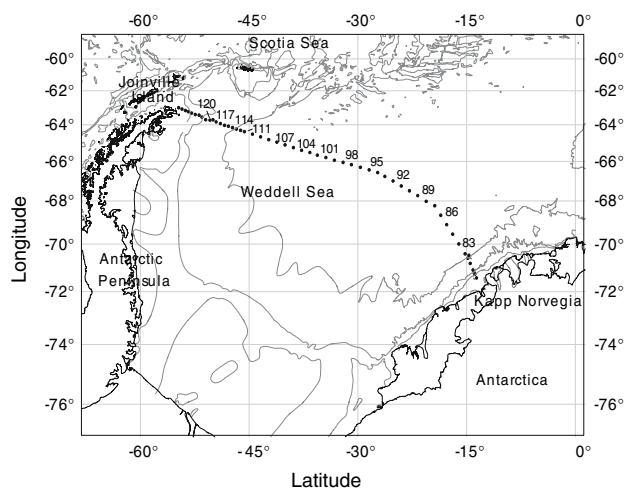


Fig. 1 Map of the Weddell Sea with the isobaths of 500, 2,000 and 4,000 m showing station positions for FS Polarstern expedition ANT XXII/3 only within the Weddell Sea for the period 24 February–11 March 2005

Total CO₂ (TCO₂), also known as total dissolved inorganic carbon (DIC), was measured with an automated coulometric and CO₂ extraction system designed after Robinson and Williams (1992). All analyses, almost all in duplicate, were performed within 24 h, but the majority within 12 h of sampling. Prior to analysis the samples were stored in the dark, and the analysis was done at a temperature close to the in situ temperature of the sample. Standardization was carried out with certified reference material (DOE 1994), batch 66 (2004) obtained from Prof. A. Dickson of Scripps Institution of Oceanography (USA). The precision, determined at a calibration station where all 24 bottles were fired at the same depth, was 0.7 μmol kg⁻¹. Due to minor differences in adjustment or occasional problems with the equipment this high precision was probably not achieved at all stations. The macronutrients nitrate, phosphate and silicate were determined with a Technicon TRAACS 800 rapid flow autoanalyzer of the Royal Netherlands Institute for Sea Research (NIOZ, Texel). Samples were either measured immediately or stored in the dark at 4°C for no longer than 24 h. Accuracy was set by stock standards diluted in low-nutrient sea water, which had been prepared in the home lab by weighing. Precision as estimated at the calibration station was 0.013 μmol l⁻¹ for phosphate, 0.07 μmol l⁻¹ for nitrate and 0.66 μmol l⁻¹ for silicate. All data were post-processed and screened for possible outliers.

Depletions

The measured concentrations are used to calculate depletions (or deficits) of TCO₂ (C), nitrate (N), phosphate (P) and silicate (Si). Previously depletions have been applied by some of us to estimate primary productivity in the western

and central Weddell Sea (Hoppema et al. 2000) using Polarstern data from December 1992/January 1993, i.e. during the height of the summer season. All details about the method and its assumptions can be found there. We compare our new depletion data with these earlier depletion data, that were collected along exactly the same transect through the Weddell Sea. Other investigators have applied the method in different regions of the Southern Ocean (Le Corre and Minas 1983; Ishii et al. 1998; Rubin et al. 1998; Carillo and Karl 1999). Briefly, the temperature minimum depth for each station was established from CTD profiles, while depletions were computed only for stations with temperature $<-1.6^{\circ}\text{C}$ in the temperature minimum—the total number of stations for which this holds is 26. For stations without a clear temperature minimum layer, depletions could not be computed—this holds for some shallower stations off Joinville Island in the west. Before the analysis, all concentrations (c) of parameters were normalized to a salinity (S) of 34.5 according to $c_{\text{norm}} = c (34.5/S)$. This corrects for changes in the concentrations due to spatially varying dilution with meltwater, which would otherwise modify the concentrations and results. For all parameters, the differences between the property value in the temperature minimum and that at the other depths were plotted against depth (Middag 2005). Then the integral versus depth was computed which represents the depth-integrated depletion. Accounting for the density of the surface water (taken to be $1,027.6 \text{ kg m}^{-3}$) and the entire surface layer depth of 50–75 m (depending on

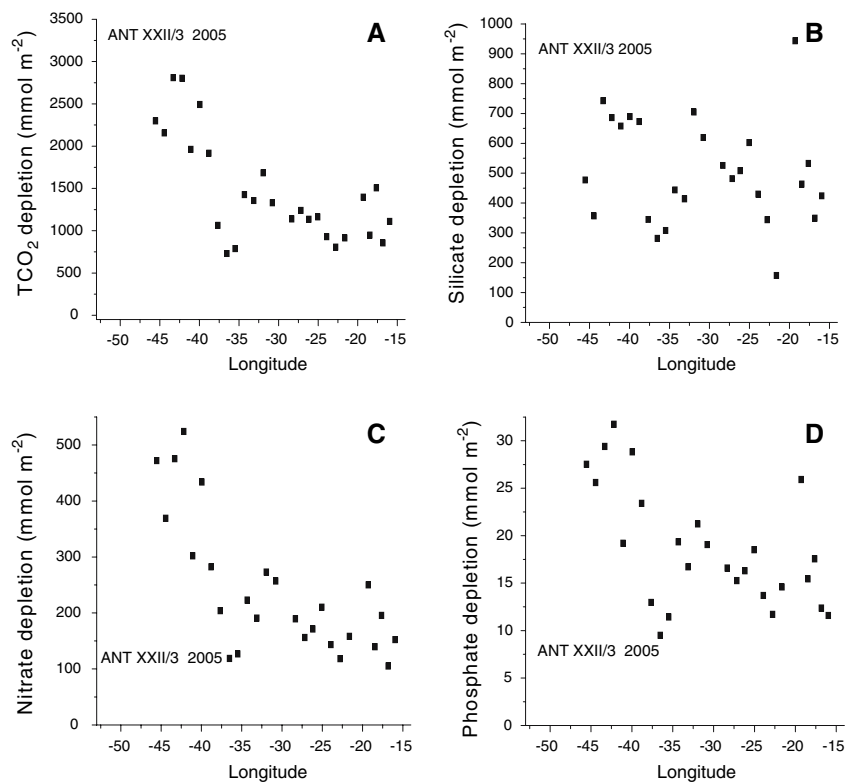
the station) produces depletions in the unit mol m^{-2} . Depletion ratios presented further in the paper are the quotients of the depletions per station.

Depletions represent the time-integrated changes of the entire surface layer from the winter until the moment of sampling. Changes in the surface layer are primarily caused by biological uptake, but also by physical processes that may distort the structure of the upper water column, such as advection, vertical mixing and upwelling. In the interior Weddell Sea the current velocities are relatively small (Fahrbach et al. 1994), and thus advection is not expected to play a big role. The practical criterion for physical processes to be negligible in the Weddell Sea is that the temperature minimum layer, which occurs all through the subpolar regime and represents a remnant of the previous winter, should be close to the freezing point (which is the temperature of the surface layer in winter). As noted above, only stations that fulfill this criterion were selected for the analysis.

Results and discussion

Surface layer deficits are presented in Fig. 2 as a function of geographical longitude along the Weddell Sea transect for austral autumn 2005. It is apparent that the spatial distribution of the different parameters along the transect is similar. For example, there is a local depletion maximum for all

Fig. 2 Depletions of **a** TCO_2 , **b** silicate, **c** nitrate and **d** phosphate (all in mmol m^{-2}) as a function of longitude for the transect across the Weddell Sea for cruise ANT XXII/3 in March 2005



parameters near 32°W, a minimum near 36–37°W and the absolute maximum near 42°W. This should not come as a surprise because the utilization of CO₂, nitrate and phosphate by phytoplankton is coupled. For the silicate uptake this is slightly different, because silicate is only utilized by some specific phytoplankton species, of which diatoms are by far the most important. The fact that the spatial distribution of the silicate depletion conforms to that of the other nutrients is a first indication to the importance of diatoms in the phytoplankton population of the Weddell Sea. Nutrient deficits towards the western margin (38–45°W) are considerably larger than those in the more central portions of the Weddell Sea (see also Table 1), this being less obvious for the silicate deficit. This may be related to water exchange processes involving nearby shelf and slope waters, but also a shorter duration of ice coverage may play a role. Biological activity in shelf and slope waters is usually higher than in the open ocean waters of the Antarctic (Mathot et al. 1992).

Along the same transect across the Weddell Sea, depletions of TCO₂, nitrate, phosphate and silicate are shown for the austral summer (December 1992/January 1993) as a comparison (Fig. 3). These data were previously discussed in Hoppema et al. (2000). Similar to the March 2005 data, there is a congruency of the spatial distributions of the C, N and P depletions, with a depletion maximum near 37–38°W, a minimum near 43–46°W and the absolute maximum close to the coast (>50°W). Although some of these features can also be seen in the distribution of Si depletion, there is less overall agreement. For example, at the aforementioned maximum near 37–38°W there is no corresponding maximum of the Si depletion; a maximum of the Si depletion occurred near 42°W. Also at some locations

the Si deficit is very close to zero. This indicates that in December 1992/January 1993 the dominance of diatoms was certainly not as large as in March 2005. The importance of non-siliceous phytoplankton early in the season was also indicated by Leynaert et al. (1993) with data from the same region.

It is striking that the general level of deficits is significantly higher in March 2005 (Fig. 2; Table 1) than in December/January 1992/1993 (Fig. 3). For the central Weddell Sea (excluding the high values in the near-margin region), the TCO₂ depletion was 1,000–1,500 mmol m⁻² in 2005, but only about 500 mmol m⁻² in 1992/1993. Similarly, the N depletion (P depletion) was 150–200 mmol m⁻² (15 mmol m⁻²) in March against 50–100 mmol m⁻² (5–10 mmol m⁻²) in December/January. Also for the Si depletion the values are at least twice as high in March 2005 as compared to December/January 1992/1993. In the margin-adjacent region (38–45°W) the difference of the depletions in March 2005 and in January 1993 was a factor of 3–5 higher than the corresponding difference in the central Weddell Sea. There are two main causes for the higher depletions in March 2005 as compared to December 1992/January 1993: First, inter-annual variability of phytoplankton activity may be very large, and second in December/January 1992/1993 the vegetative season may have been in an earlier stage than in March 2005, implying that the biological uptake of nutrients had not yet reached its potential maximum that early in the season. Note that the first cause is actually a composite one, which includes e.g. variable ice conditions and stratification—these in turn affect the phytoplankton variability. If the second cause were dominant, this would suggest that in late summer (i.e., after mid-January, when the 1992/1993 cruise ended) the biological uptake of nutrients continues. This is in contrast to the ecosystem west of the Antarctic Peninsula, where later than January no significant biological drawdown of nutrients was observed (Karl et al. 1991). Note that the SeaWiFS chlorophyll data (at <http://oceancolor.gsfc.nasa.gov> of NASA, USA) for the Weddell region, though only showing the near-surface chlorophyll, have the highest values in February. This is an indication that at least some biological drawdown of nutrients occurs also later than January.

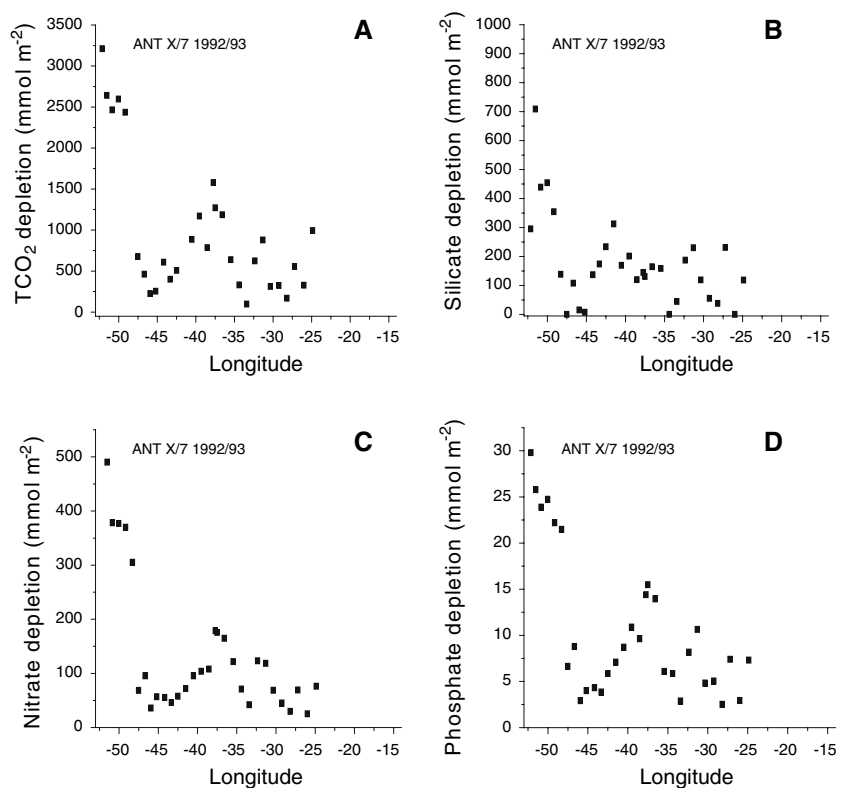
Estimate of net community production

If we assume that the TCO₂ depletion be solely generated by biological utilization, the net community production (NCP) during the season can be estimated in terms of carbon units. NCP is the primary production of autotrophs (mostly phytoplankton) reduced by the respiration of the whole community, mostly of heterotrophs (like bacterioplankton or zooplankton) (Williams 1993). As a first estimate for the NCP, it is simply equal to the TCO₂ depletion, namely

Table 1 Mean depletions and depletion ratios (\pm standard error) for two subregions of the Weddell Sea along the transect from Kapp Norvegia to Joinville Island for cruise ANT XXII/3 in 2005

	Central Weddell Sea	Western near-margin
	Depletion (mmol m ⁻²) or ratio	Depletion (mmol m ⁻²) or ratio
Longitude; number of stations	16–38°W; <i>N</i> = 19	38–46°W; <i>N</i> = 7
TCO ₂ depletion	1,133 \pm 61	2,348 \pm 139
Phosphate depletion	15.8 \pm 0.9	26.5 \pm 1.6
Nitrate depletion	178 \pm 11	408 \pm 35
Silicate depletion	467 \pm 40	612 \pm 53
N:P depletion ratio	11.3 \pm 0.4	15.3 \pm 0.6
C:P depletion ratio	72.6 \pm 2.3	76.6 \pm 11.5
C:N depletion ratio	6.5 \pm 0.2	5.9 \pm 0.2
C:Si depletion ratio	2.6 \pm 0.2	4.0 \pm 0.4
Si:N depletion ratio	2.6 \pm 0.1	1.6 \pm 0.2

Fig. 3 Depletions of **a** TCO_2 , **b** silicate, **c** nitrate and **d** phosphate (all in mmol m^{-2}) as a function of longitude for the transect across the Weddell Sea for FS Polarstern cruise ANT X/7 in December 1992/January 1993. Data previously reported in Hoppema et al. (2000)



$1.1 \pm 0.1 \text{ mol C m}^{-2}$ ($= 14 \pm 1 \text{ g C m}^{-2}$) for the central Weddell Sea, and $2.4 \pm 0.1 \text{ mol C m}^{-2}$ ($= 28 \pm 2 \text{ g C m}^{-2}$) for the near-margin area. However, TCO_2 depletions and thus NCP are underestimated because of additional CO_2 -modifying processes that take place unrelated to photosynthesis and degradation of organic matter. We consider two processes which are thought to be significant, first, CO_2 uptake from the atmosphere during the summer season, and second, changes associated with calcium carbonate (CaCO_3). Their contributions are estimated below.

CO_2 uptake from the atmosphere occurs during the summer season because of CO_2 undersaturation in the surface water induced by biogenic CO_2 utilization. Other investigators have estimated the effect of atmospheric CO_2 on the TCO_2 deficit in the surface layer and concluded that the contribution is non-negligible but $<10\%$ of the TCO_2 depletion (Rubin et al. 1998; Carillo and Karl 1999; Sweeney et al. 2000). However, from the work of Ishii et al. (1998) a higher percentage can be deduced, and this also holds true for other regions like the Baltic, where the contribution is on the order of 30% (H. Thomas and Schneider 1999). As regards the Weddell Sea, in a previous investigation the annual mean CO_2 uptake in its interior was calculated to be $3.6 \mu\text{mol kg}^{-1}$ (Hoppema et al. 1999). If this uptake would be brought about by a mixed layer of 50 m depth, this would reduce the depletion by about 0.2 mol m^{-2} . However, it is unlikely that all CO_2 uptake will occur during summer with relatively low wind speeds. Although the

autumn period is short, a substantial part of the uptake occurs in this time of the year because of the high wind speeds. Tentatively, we assume that half of the annual CO_2 uptake occurs during the summer, i.e. the correction for air-sea exchange of CO_2 amounts to 0.1 mol m^{-2} .

Another potentially significant modifying process is the formation and/or dissolution of CaCO_3 particles in the surface layer. Here we should distinguish two different aspects. The first is the formation and dissolution of CaCO_3 by calcareous plankton in the surface layer. In the Weddell Sea the abundance of calcareous plankton in the surface layer and in sediment traps below it is relatively small (Fischer et al. 1988)—indeed, the Southern Ocean phytoplankton population is dominated by siliceous species, mainly diatoms. Chemical evidence for this may be provided by alkalinity data because CaCO_3 changes are reflected in changes of the alkalinity. In several investigations in the Southern Ocean, sea surface alkalinity was found to behave conservatively (e.g., Bates et al. 1998), i.e. variations could be explained solely by changing salinity (dilution). We conclude that this kind of influence of CaCO_3 is not very significant. Moreover, it should be stressed that the only effect of such CaCO_3 variations on the depletion would be to change the TCO_2 concentration without changing the other nutrients and thus invalidate the Redfield ratios of nutrient utilizations.

The second aspect of CaCO_3 chemistry concerns precipitation and dissolution of CaCO_3 during sea-ice formation

and melting. Accompanying sea-ice formation, brine is formed from which CaCO_3 precipitates. Whereas the brine is released into the surface water, most CaCO_3 is contained in the ice. Thus during ice formation the alkalinity of the surface mixed layer is reduced, whereas during ice melting in the next spring it is elevated due to dissolution of CaCO_3 from the ice (Jones et al. 1983). The potential consequences for depletion calculations are as follows: The dissolution of CaCO_3 in spring increases not only alkalinity but also the TCO_2 concentration of the layer overlying the temperature minimum. This process occurs also after the onset of algal production and thus the algal CO_2 consumption estimated from the TCO_2 depletion (which is calculated from the difference between the concentration in the temperature minimum and the layer above it) will be underestimated. Jones et al. (1983) have shown that the effect on the surface water alkalinity in Baffin Bay in the Arctic is substantial. For the Southern Ocean contradictory evidence is found in the literature—here we focus on data which include both the sea surface and the temperature minimum layer. Karl et al. (1991) emphasized that alkalinity did not show signs of CaCO_3 changes in Gerlache Strait. Anderson et al. (1991) and Poisson and Chen (1987) reported alkalinity to behave conservatively in the Weddell Sea. In contrast, Weiss et al. (1979) showed the alkalinity of Summer Surface Water to be $28 \mu\text{mol kg}^{-1}$ higher than that of the underlying Winter Water (= temperature minimum layer). As Jones et al. (1983) suggested, this may well be due to meltwater impact. Sweeney et al. (2000) show alkalinity in the Ross Sea to be more variable ($\pm 16 \mu\text{mol kg}^{-1}$) in the surface layer than in the deeper waters, and ascribe this to CaCO_3 . In the Weddell Sea, alkalinity has an uncertainty of about $10 \mu\text{mol kg}^{-1}$ (Poisson and Chen 1987). If we adopt a variation of alkalinity in the range $10\text{--}16 \mu\text{mol kg}^{-1}$, this translates into a TCO_2 change of $5\text{--}8 \mu\text{mol kg}^{-1}$, the TCO_2 changes being half those of alkalinity. We assume this to be the amount by which the TCO_2 depletion has been underestimated. One may note that we use the spread of the alkalinity distribution to come an estimate of alkalinity increase. This is done because CaCO_3 dissolution during ice melting is the only possible source of alkalinity increase. In addition, data of Weiss et al. (1979) do indicate the existence of alkalinity increases. As to the range chosen, note that the magnitude of alkalinity change due to meltwater is dependent on the kind of ice, its thickness, age and advection. The central Weddell Sea is annually covered by first-year ice, and thus impact in the central Weddell Sea may not be that large as suggested by Weiss et al. (1979). If the estimated $5\text{--}8 \mu\text{mol kg}^{-1}$ of TCO_2 is distributed over a summer surface layer of 50 m, the underestimation of the TCO_2 depletion becomes $0.25\text{--}0.4 \text{ mol m}^{-2}$.

In sum, CO_2 uptake from the atmosphere contributes about 0.1 mol C m^{-2} to the underestimation of the TCO_2

depletion, and CaCO_3 dissolution may contribute some $0.25\text{--}0.4 \text{ mol C m}^{-2}$. This yields the NCP for the period until March 2005 to be about $1.5 \pm 0.2 \text{ mol C m}^{-2}$ ($= 18 \pm 2 \text{ g C m}^{-2}$) for the central Weddell Sea, and $2.8 \pm 0.2 \text{ mol C m}^{-2}$ ($= 34 \pm 2 \text{ g C m}^{-2}$) for the near-margin area. These relatively low values agree quite well with NCPs computed from surface layer deficits along the coasts of Enderby Land and Wilkes Land in East Antarctica (Ishii et al. 1998) and in the Scotia Sea (Shim et al. 2006). On the other hand, across the Ross Sea including the Ross Sea Polynya (Sweeney et al. 2000), and in the Gerlache Strait west of the Antarctic Peninsula (Karl et al. 1991; Serebrennikova and Fanning 2004), much higher depletions and NCPs have been found.

Our measurements were performed towards the end of the vegetative season, so we regard the estimated NCP to be close to the annual maximum. However, there has been more production after our cruise in March, and so we must consider the above as underestimates. We tentatively estimate the effect on the NCP as follows. Since the seasonal pack ice is so dominantly determining the complete ecosystem, we assume that productivity will continue at the mean rate until the ice pack closes. Satellite images of the ice coverage indicate that the Weddell Sea was closed by about mid-April (<http://www.seaice.de> of the University of Bremen, Germany), i.e., one month after our measurements. To the estimated NCP of 1.5 mol m^{-2} for the interior Weddell Sea, which has been brought about during a period of about 4 months (from mid-November to mid-March), we have to add another $0.3\text{--}0.4 \text{ mol C m}^{-2}$ to cater for the productivity of one month after mid-March. Hence the total annual NCP for the vegetative season is estimated at $1.8 \pm 0.3 \text{ mol C m}^{-2} \text{ year}^{-1}$ ($= 22 \pm 4 \text{ g C m}^{-2} \text{ year}^{-1}$). Applying the same procedure to the near-margin region, we arrive at an annual NCP of $3.5 \pm 0.3 \text{ mol C m}^{-2} \text{ year}^{-1}$ ($= 42 \pm 4 \text{ g C m}^{-2} \text{ year}^{-1}$).

In summary, the NCP of the central Weddell Sea amounts to 1.5 mol C m^{-2} for the period until mid-March. An additional estimated contribution for autumnal production may increase it to about 1.8 mol C m^{-2} . Since the NCP represents the amount of net carbon production in the surface layer that is available for downward transfer, its value may be compared with the export production, the more so as we claim to have captured almost the entire annual NCP of the vegetative season. The annual export production in the central Weddell Sea, determined from a nutrient balance of the surface and subsurface layers, was reported to be $21 \pm 4 \text{ g C m}^{-2} \text{ year}^{-1}$ ($= 1.7 \text{ mol m}^{-2} \text{ year}^{-1}$) (Hoppema et al. 2002) which is insignificantly different to our estimate of NCP. However, this may be fortuitous. Our autumnal estimate for NCP actually may be lower since the primary production in autumn is probably lower than during the height of the season (Arrigo et al. 1998)—indications for

this can be found in the (highly incomplete) satellite chlorophyll data (SeaWiFS) for March and April 2005 in the Weddell Sea. On the other hand, there is production in winter, which, though low (Spiridonov et al. 1996; Cota et al. 1992), may well be 10% of the total for the pelagic region (Arrigo et al. 1998). Also some productivity may occur during some weeks associated with new sea-ice formation (Gleitz and Thomas 1993). Finally, a very important factor is inter-annual variability, which may be large in the Southern Ocean (Smith et al. 2006). Therefore, the NCP for 2005 need not be consistent with the export production from other years.

Although we cannot say for sure whether the NCP determined for 2005 be higher or not than the export production, these two parameters are not very different. This implies that the degradation of organic matter in winter under the ice cannot be very intensive. One might encounter that the dissolved oxygen concentration in the surface layer at the end of the winter is strongly undersaturated (Gordon and Huber 1990), and attribute this to biological activity. However, the latter authors have shown that this undersaturation can be fully explained by entrainment into the surface layer of strongly oxygen-undersaturated subsurface water. This supports the findings of the present investigation.

Smith and Nelson (1990) report a high new production for the Weddell Sea of $49 \text{ g C m}^{-2} \text{ year}^{-1}$ ($= 4.1 \text{ mol m}^{-2} \text{ year}^{-1}$). Although new production and NCP are fundamentally different properties, the high new production still seems hard to reconcile with our low estimate of NCP. However, their value includes the marginal ice zone north of our section and both the SeaWiFS satellite and our own data show that towards the margin chlorophyll and NCP increase dramatically (see also Hoppema et al. 2000). Thus this appears to fit in the larger picture of the Weddell Sea. The bottom line is that one should be cautious to extrapolate marginal ice zone data to the entire Weddell Sea.

Biogenic silicate production

The silicate depletion may be used to estimate the net biogenic silica production, which yields $0.5 \text{ mol Si m}^{-2} \text{ year}^{-1}$ for the central Weddell Sea and $0.6 \text{ mol Si m}^{-2} \text{ year}^{-1}$ for the near-margin region. These estimates are comparable in magnitude to some earlier estimates given for the Weddell region (e.g., Jennings et al. 1984; Van Bennekom et al. 1988; Leynaert et al. 1993). These net estimates are not to be confused with the gross rate of biosilicification which is much higher, the difference being due to remineralization of biogenic opal within the upper water layer. Beucher et al. (2004) reported intense silicon recycling within the surface layer, where virtually the complete biogenic silica production can be dissolved during the summer. It has been long

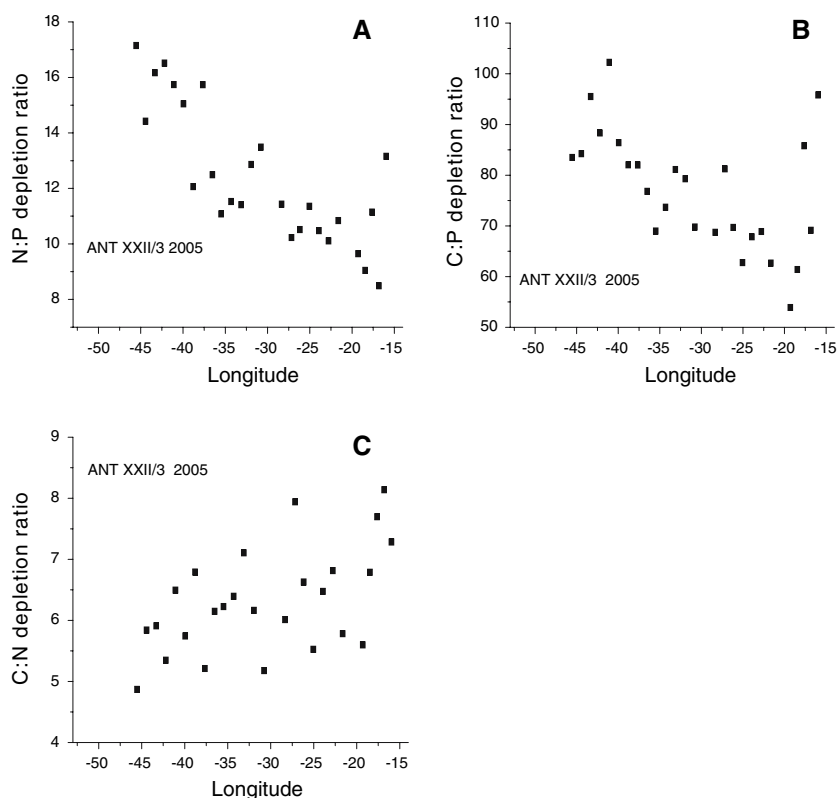
known indeed that the dissolution rate of silica of Antarctic diatoms is relatively high due to their very low Al:Si ratio (e.g., Van Bennekom et al. 1988). Additionally, in the data of Gibson and Trull (1999), which exhibit true seasonal cycles, it can be seen that the silicate concentration returns almost to its pre-bloom level within the two months of January and February. Since our measurements were performed towards the end of the vegetative season, dissolution will have taken place, which will lead to a modest net estimate of silicate removal versus the gross seasonal silicate consumption.

Nutrient depletion ratios

The absolute magnitude of depletion is a very useful measure for net biological consumption integrated over the preceding growing season. With depletion ratios of different nutrients, additional information on the prevailing conditions may be obtained, both biological and geochemical. Several depletion ratios involving C, N and P are shown across the Weddell Sea for March 2005 (Fig. 4). In the central Weddell Sea the N:P depletion ratio exhibits a range of 9–13 (Fig. 4a), which is lower than the N:P ratio of about 14 prevailing further north in the Atlantic sector of the Southern Ocean (De Baar et al. 1997). Only in the near-margin region (38–45°W) the values are higher and approaching the canonical Redfield ratio N:P = 16. For the 1992/1993 data higher N:P ratios were found (Hoppema and Goeyens 1999) than in March 2005, but this includes both central part and Weddell Sea margin data, where the latter tend to enhance the mean N:P ratio. N:P utilization values clearly under 16 appear to be no exception in the Southern Ocean (Korb and Whitehouse 2004; Shim et al. 2006). Also the C:P depletion ratios are lower in the central Weddell Sea than in the near-margin region (Fig. 4b). The mean of the ratio is, like that of N:P, much lower than the classical Redfield ratio of 106, and also lower than the C:P ratios from 1992/1993 (Hoppema and Goeyens 1999). For the C:N depletion ratios the situation is different, with lower values in the near-margin region than in the central Weddell Sea. The means are, contrary to the other ratios, close to the classical Redfield C:N ratio of 6.6 as well as close to those from 1992/1993.

Except for the mean C:N depletion ratios, the mean C:P and N:P ratios in March 2005 are significantly lower than the classical Redfield ratios (Table 1). This is different from January 1993, when the depletion ratios were generally in agreement (though somewhat lower) with the Redfield model (Hoppema and Goeyens 1999). But maybe referring to the Redfield model is not appropriate here. Arrigo et al. (1999) reported a huge difference in N:P disappearance ratios for diatoms and *Phaeocystis* dominated waters in the Ross Sea amounting to 9.7 and 19.2, respectively.

Fig. 4 Depletion ratios of **a** nitrate:phosphate, **b** carbon:phosphate and **c** carbon:nitrate as a function of longitude for the transect across the Weddell Sea for cruise ANT XXII/3 in March 2005



Similarly, large differences in C:P disappearance ratios were found, namely, 94 and 147, respectively. The C:N ratios for these differently populated waters were similar but with 8–9 clearly higher than the canonical one. It should be noted that Arrigo et al. (1999) use nitrate as the nitrogen species, and not total nitrogen (i.e., including ammonium and nitrite). For comparison purposes we also use the nitrate depletions.

The low N:P ratios and C:P ratios found in the Weddell Sea (Table 1) thus seem to point to a diatom-dominated uptake of nutrients. In the near-margin area the N:P and C:P ratios were the highest (Fig. 4), hence non-diatoms may play a significant role there as well. This spatial distribution appears to be in agreement with phytoplankton studies in the Weddell Sea (e.g., Krell et al. 2005). An apparent paradox is that in the near-margin area where non-diatoms are significant, the Si depletion is the highest of the entire transect (Fig. 2). The simple explanation is that the overall biological utilization (represented by the C, N and P deficits) is about a factor 2 higher in the near-margin area than in the central Weddell Sea, and the Si depletion simply complies with this. We note that the C:P and C:N ratios in the Weddell Sea are lower than those in the diatom-dominated waters of the Ross Sea. The obvious reason for this is the underestimation of the TCO_2 depletion. If a correction term of 0.4 mol m^{-2} would be added to TCO_2 depletions (see above), this would bring the C:P and C:N depletion ratios close to those for diatom dominated waters (sensu

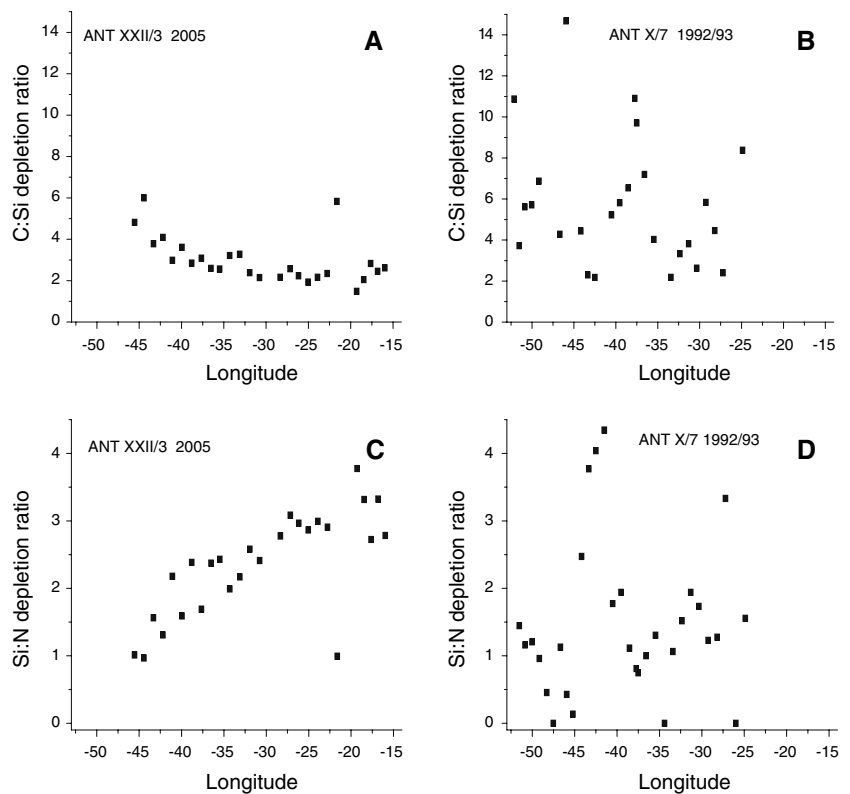
Arrigo et al. 1999). This is a very strong additional indication that the correction term for the TCO_2 depletion is necessary. The spatial distribution of ratios is not influenced by this correction. Finally, with respect to ratios involving CO_2 it should be realized that deviations from Redfield ratios are likely because nitrate and phosphate are taken up by phytoplankton, whereas CO_2 is utilized not only by phytoplankton but also released by heterotrophs (Banse 1994). Hence, values close to the canonical Redfield ratios may point to low heterotrophic activity in the surface layer.

Iron control

Iron is now well-known to be a main factor for controlling primary production in the Southern Ocean (e.g., De Baar et al. 1990; Martin et al. 1990). Unfortunately iron concentrations were not measured during our cruise. However, we can still speculate about iron control by considering C:Si and Si:N depletion ratios. For this we make use of the spectacular results gathered under experimental conditions that diatoms under Fe-deficient conditions consume much more silicate than under Fe-replete conditions (Takeda 1998). Thus under Fe-deficient conditions the C:Si ratio will be lower and the Si:N ratio will be higher than under Fe-replete conditions.

We shall use the C:Si and Si:N depletion ratios (Fig. 5) only for comparing and not for discussing the absolute values. As regards the underestimation of the TCO_2 deficit,

Fig. 5 Depletion ratios of **a, b** carbon:silicate, and **c, d** silicate:nitrate for the transect across the Weddell Sea for cruises ANT XXII/3 in March 2005 (*left*) and ANT X/7 in January 1993 (*right*)



this will be very similar for two different years and thus largely cancel out in the comparison. The general picture is that the level of C:Si ratios is clearly higher and the Si:N ratios are generally lower in January 1993 than in March 2005. Hence, the conclusion must be that in January 1993 the Fe stress was less than in March 2005. Higher Fe stress in March could be caused by Fe utilization by the phytoplankton earlier in the season. Seasonal iron limitation towards the end of the vegetative season was also demonstrated in the Ross Sea and it exerts control on phytoplankton growth (Sedwick et al. 2000). In the near-margin region (38–45°W) the C:Si ratios are higher, while the Si:N ratios are lower than further to the east in the central Weddell Sea (Fig. 5a, c). This indicates that in the near-margin region the Fe stress is less and consequently the NCP higher (Table 1) than in the adjacent Weddell Sea interior. The regional differences in Fe availability thus likely exert control on the sustained level of primary production in the Weddell Sea. Fe concentrations near the margins may be higher because of mixing or advection of shelf waters with high Fe concentrations (Westerlund and Öhman 1991).

Concluding remarks

The net community production in the central Weddell Sea, representative for the vegetative season only, was found to be low with about $1.8 \text{ mol C m}^{-2} \text{ year}^{-1}$. Fortuitous or not,

this value is not very different from the reported export production for the central Weddell Sea (Hoppema et al. 2002). In austral autumn and winter, remineralization of organic matter produced in the preceding period will occur in the surface layer, which will reduce the NCP to its real annual value, which in turn should be equal to the annual export production. This would thus suggest that degradation of organic matter in winter under the ice be relatively minor.

The central Weddell Sea is affected by the seasonal advance and retreat of the pack ice, which classifies it as a marginal ice zone region. Although the marginal ice zone has been propagated as a region of enhanced productivity due to meltwater stabilization of the water column (Smith and Nelson 1985), the central Weddell Sea does not seem to align with this theory, given the low NCP. For some nearby regions, contradictory reports were published. While Smith and Nelson (1990) found elevated production in the northern Weddell Sea, Bathmann et al. (1997) report the absence of blooms in the southern Antarctic Circumpolar Current. Savidge et al. (1996) conjecture that sheltered areas with a closed circulation would be beneficial for the occurrence of ice-edge blooms, but the present Weddell Sea data and those of Smith and Nelson (1990) pose an apparent paradox with respect to that contention, as the central Weddell Sea is more sheltered. Iron availability may help solving the paradox. While the central Weddell Sea is pinched off of major iron inflow, the northern Weddell Sea, being situated downstream of the Antarctic Peninsula,

might receive iron from the shelves. More work is needed to resolve this issue.

Although we did not have iron measurements to our availability, we tentatively deduced that Fe deficiency may be an important factor for keeping the phytoplankton growth relatively low in the Weddell Sea interior, whereas towards the margin the Fe stress gets lower, allowing higher production. The extent of Fe-depleted areas might increase in the course of the vegetative season. With regard to biological production, the following differentiation pertains to the Weddell Sea. In the central part it is low (this study) due to low Fe availability. Around the central part is a near-margin region, situated approximately over the continental slope, with production about twice as high. Here water exchange processes with fertile shelf waters may take place, or enhanced upwelling of Fe-rich deeper water through topography–circulation interactions. Finally there are the shelves with their fertile waters, caused by high Fe concentrations. Frequent polynyas additionally extend the time period of open water necessary for high production to occur.

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