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Intense nutrient removal in the remote area off Larsen Ice Shelf (Weddell Sea)

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Abstract Using Weddell Sea data collected during a cruise with "FS Polarstern" in austral summer 1992/1993, depletions of nutrients and TCO_2 in the summer surface layer were calculated. The analogous depletion-like properties for temperature (Heat Storage) and salinity were also computed. The latter properties are useful to describe the physical conditions over the time period pertinent to the depletions. For different areas a strong correlation exists of Heat Storage and nutrient/TCO_2 depletions, which is caused by a common factor – the period of light availability. Offshore of the Larsen shelf, an area usually inaccessible due to perennial ice cover, high nutrients/TCO_2 depletions are achieved over a short period of time, pointing to a rapidly producing biological system. Primary productivity, calculated from the TCO_2 depletion, amounts to about 100 mg C m^{-2} day^{-1} for the central Weddell Sea, but 570–1140 mg C m^{-2} day^{-1} for the offshore Larsen region. These values agree fairly well with the open-ocean Antarctic and other coastal areas, respectively.

Introduction

Although carbon dioxide (CO_2) is a minor component of the atmosphere, the issue of its steadily rising atmospheric concentration has stimulated much interest, because this may lead to an enhanced greenhouse effect with accompanying adverse environmental and economical effects. CO_2 is a natural and essential component of the atmosphere, which plays a pivotal role in the heat budget of the earth surface. CO_2 is also required for photosynthesis. Marine primary production and the subsequent CO_2 undersaturation in the euphotic surface layer induce CO_2 removal from the atmosphere. In order to assess the CO_2 sequestration effect of oceanic photosynthesis, a better understanding of the oceanic biological cycles and the physical and chemical factors governing them is necessary. Within the oceanic realm, the Southern Ocean has a special position due to its outstanding biogeochemistry, of which the nutrient-replete surface water is an especially remarkable exponent.

It has long been established that a strong correlation exists between the onset and intensity of phytoplankton blooms and favourable physical conditions such as sufficient light availability, shallow depth of the mixed layer, and nutrient abundance in the oceanic surface layer (Sverdrup 1953). In the Antarctic, the ubiquitous abundance of nutrients alone does not always connote a high primary production. Productivity in Antarctic waters varies from oligotrophic levels in the open ocean (El-Sayed and Weber 1982; Jacques 1989) to eutrophic levels in the wake of the receding pack ice and in sheltered coastal embayments (von Bodungen et al. 1986; Karl et al. 1991), the variability spanning over 2 orders of magnitude (Mathot et al. 1992). Moreover, the apparent paradox between poor primary production and high standing stocks of higher trophic levels promoted the paradigm of the Antarctic food web, which emphasizes the role of pico-, nano- and microplankton producers and predators, as well as bacterial secondary producers (El-Sayed 1987). Long-existing fundamental knowledge in combination with the recent intensification of research efforts unveiled that different physicochemical, as well as biological, controls can govern Antarctic primary production (Smith and Nelson 1985; Veth et al. 1992) and that the Southern Ocean cannot be regarded

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as one unique ecosystem with uniform functional characteristics throughout (Tréguer and van Bennekom 1991). According to Tréguer and van Bennekom (1991), one can distinguish five different subunits: the permanently open-ocean zone, the Polar Front zone, the seasonal ice zone, the coastal and continental shelf zone and the permanent ice zone. Both intrazonal and interannual variability, however, may frustrate a rigid subdivision. Even the permanent ice zone, which seems to be a persistent feature, is not as permanent as the term suggests. We experienced this during the 1992/1993 summer period, when the steady pack ice off the Larsen Ice Shelf was not found to be present.

The present study aims at a better insight into the spatial variability of biologically mediated nutrient and CO_2 removal in the Weddell Sea. Surface layer depletions are used, which allow for reliable estimates of primary productivity and shortcut possible bias due to the inherent seasonal variation and natural patchiness of the processes involved. Traditional measurements might fail to include significant contributions of episodic events such as superblooms (Smetacek et al. 1992), whereas the depletion method inherently accounts for this. Relationships between biological parameters and hydrography have been investigated in the Weddell region (e.g. Nelson et al. 1987; Scharek et al. 1994). We use a new approach, applying physical parameters that are calculated on the same basis as the nutrient depletions, and that are therefore fully consistent with these.

An extra dimension to our investigations was the fact that we had the unique opportunity to visit an area off the Larsen Ice Shelf, which is known to be perennially ice covered. The southernmost regions along the eastern side of the Antarctic Peninsula are usually covered by a thick, multi-year ice pack, which normally does not allow ships to navigate there. During our cruise, however, the ice conditions were exceptionally favourable with large areas being ice-free, giving us the opportunity to follow the coastline of the Antarctic Peninsula and the Larsen Ice Shelf in front of it as far south as 69°S (Fig. 1). We present productivity data, calculated from uptake of CO_2 and nutrients, for this remote area, which is not likely to be visited again in the near future.

Materials and methods

Data were collected during cruise ANT X/7 of the German research vessel "FS Polarstern" in December 1992/January 1993. A suite of physical and chemical parameters was measured (Fahrbach 1994). Temperature and salinity profiles were obtained by means of a Conductivity-Temperature-Depth (CTD) instrument. The accuracies for the temperature and salinity are 3 mK and 0.003 (practical salinity scale), respectively. Water for the determination of TCO_2, silicate, nitrate and phosphate was taken from a rosette sampler coupled to the CTD.

Total CO_2 (TCO_2), which is the sum of all inorganic carbonate species dissolved in seawater, was analysed with a coulometric technique (DOE 1994). Saturated mercury-(II)-chloride was added as a preservative to the samples. All analyses were performed within 24 h, but most within 12 h of sampling. Prior to analysis, samples were stored in the dark. The mean difference of all duplicates amounts to 0.9 μmol kg^{-1}. Standardization was done with certified reference seawater (DOE 1994). TCO_2 data from this cruise have also been reported in Hoppema et al. (1995, 1997, 1998) and Wedborg et al. (1998). Silicate, nitrate and phosphate concentrations were measured using a Technicon Autoanalyzer-II-System. Samples were generally analysed immediately after

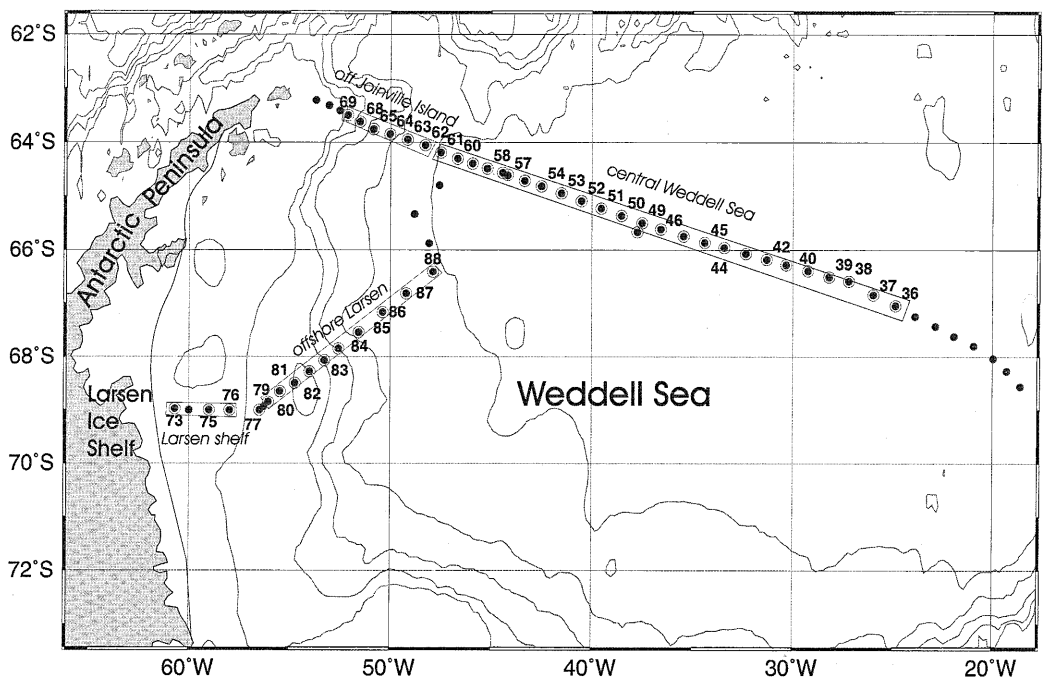


Fig. 1 Map of the Weddell Sea with station positions occupied during cruise ANT X/7. Locations of four sub-areas are depicted (see text): Larsen shelf (stations 73–76); off Joinville Island (stations 69–62); offshore Larsen (stations 79–88); central Weddell Sea (stations 36–61)

sampling. In a few cases the samples were stored, being kept in the dark at 4°C, but never for longer than 6 h. All samples were analysed in duplicate; precision was estimated at 0.3 μmol kg^{-1} for silicate, 0.1 μmol kg^{-1} for nitrate and 0.01 μmol kg^{-1} for phosphate. The accuracy was set by running four standards at the beginning and two standards at the end of each run. Part of the data was also presented by Hoppema et al. (1998).

Depletions

Our results are presented as depletions of TCO_2, nutrients, salinity and heat in the surface layer. They denote the changes in the summer surface layer with respect to the winter surface layer. Depletions can be obtained using data from a single cruise because underneath the relatively warm summer surface layer, a remnant layer of winter surface water persists just above the permanent pycnocline. The remnant winter surface water is distinguishable by its temperature minimum, which should be close to the freezing point if it is to represent a true remnant of the preceding winter surface layer. The summer surface layer can be regarded as a cap of relatively warm and salt-poor water, which keeps the remnant subsurface winter layer from direct contact with the atmosphere and prevents it being changed after the beginning of spring.

The calculated depletions represent the time-integrated changes of the entire surface layer since the end of the winter period. Previously, depletions have been applied by Le Corre and Minas (1983), Jennings et al. (1984), Goeyens et al. (1995) and Rubin et al. (1998), including Weddell Sea data. As pointed out by these authors, there are some implicit assumptions in using this methodology. The most important one is that vertical and lateral mixing in both the temperature minimum and the surface layer are small. This condition appears to be fulfilled in the Weddell Sea, where currents are weak (Fahrbach et al. 1994). The evidence for this is that the observed temperature in the temperature-minimum layer is about equal to the temperature actually observed in the winter surface layer, which is close to the freezing-point. Moreover, fluxes due to vertical gradients within the surface layer are small, as demonstrated by Goeyens et al. (1991). Possible changes of TCO_2 and nutrients due to dilution (caused by the addition of meltwater from the sea ice) are accounted for through normalization of the properties to a salinity of 35. The detailed procedure for calculating the depletions in the surface layer with respect to the temperature-minimum layer is as follows.

The temperature-minimum depth was established from the CTD profile. In some cases stations had to be discarded (off Joinville Island and at the Larsen shelf break), because the temperature in the temperature minimum greatly deviated from the actual winter value at freezing point. Then, the weighted average value of the surface layer above the temperature minimum was determined for all parameters and all stations individually. The weighting accounts for gradients of parameter values in the surface layer. With the difference of the concentrations in the temperature minimum and the weighted surface layer average (dif-X), the vertically integrated change over the entire surface water column, i.e. the depletion (dep-X), was obtained with:

$$\text{dep-X}(\text{mmol}\,\text{m}^{-2}) = \text{dif-X}(\mu\text{mol}\,\text{kg}^{-1}) * \rho(\text{kg}\,\text{dm}^{-3}) * \text{d}(\text{m}) \quad (1)$$

with ρ the density, taken 1.0276 kg dm^{-3} as a mean for all stations, d is the depth of the temperature minimum, and X a particular property. Note that this value for the density is not as accurate as it seems, because all cold seawater, as present in the Weddell Sea, has a density close to 1.027; moreover, the calculated depletion is only slightly dependent on it. For temperature a slightly modified formula was used, which is denoted here as the Heat Storage (HS) of the surface layer (actually a repletion):

$$\text{HS}(\text{kJ}\,\text{m}^{-2}) = \text{dif-T}(\text{K}) * \rho(\text{kg}\,\text{dm}^{-3}) * c_p(\text{J}\,\text{kg}^{-1}\,\text{K}^{-1}) * \text{d}(\text{m}) \quad (2)$$

where c_p is the specific heat, and kJ is kilojoule. c_p is dependent on temperature, salinity and pressure; however, in the surface layer its variation is only minor (<0.2%), and thus for all stations $c_p = 3990$ J kg^{-1} K^{-1} was taken. The term Heat Storage is used because what we calculate is that part of the heat that has remained in the surface layer. During the course of spring and summer, more heat is transferred into the surface layer, a part of which is reemitted to the atmosphere.

Results and discussion

Heat storage and salinity depletion

The spatial distribution of the Heat Storage is presented in Fig. 2, in which the distribution of the salinity depletion is also included as another physical parameter. Generally, the Heat Storage appears to be higher near the coast than further offshore, the highest values occurring on the shelf. Off the Larsen Ice Shelf, the shelf break serves as a clear division line between the high Heat Storage region on the shelf and the low region offshore. The most plausible explanation for this distribution pattern is the frequent occurrence of coastal polynyas early in the season, through which the

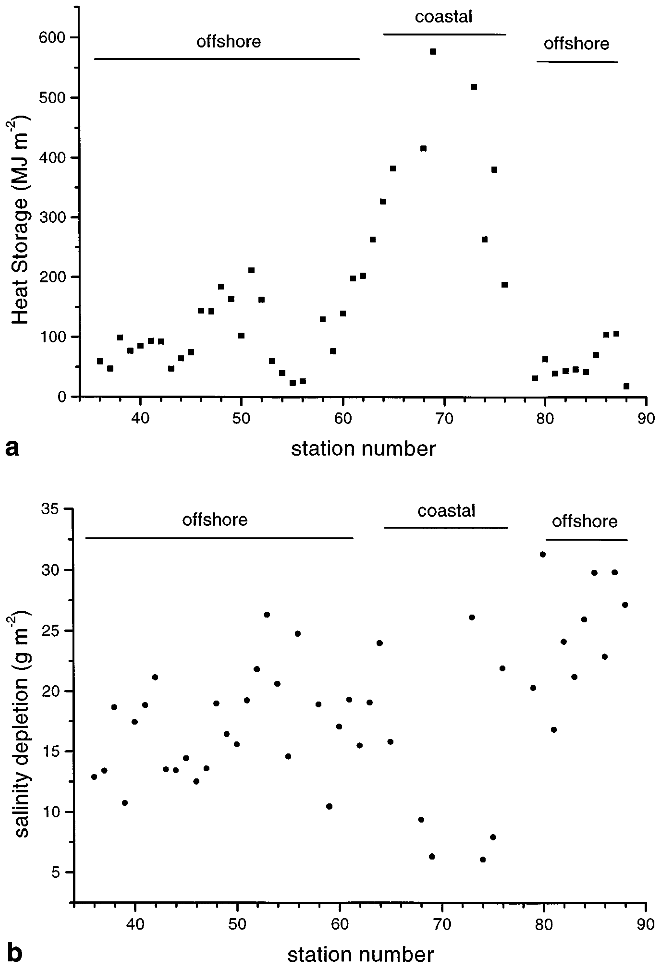


Fig. 2 Heat Storage (**A**) and salinity depletion (**B**) as a function of the geographical position (station number) in the Weddell Sea. MJ is 10^6 joule

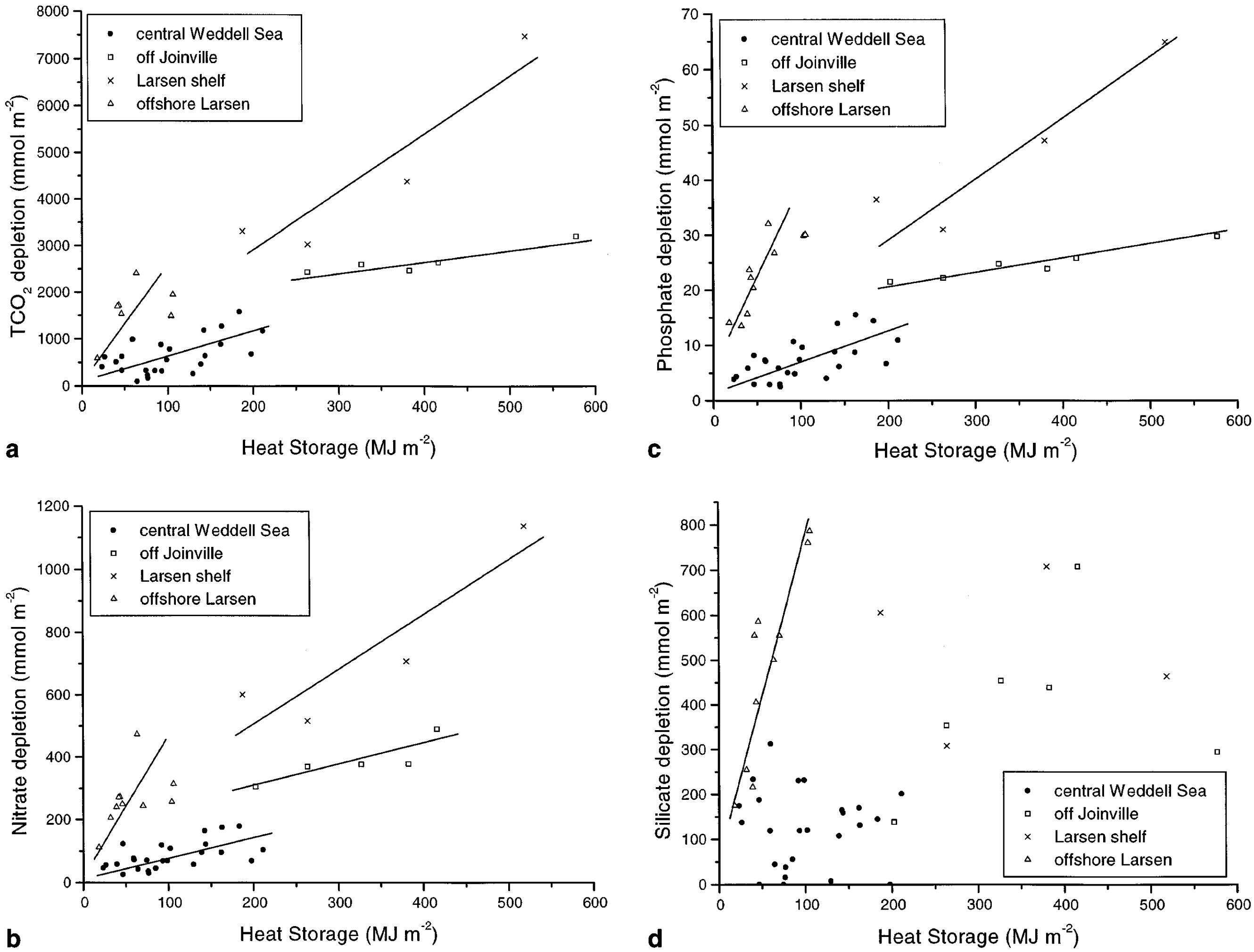
exchange of heat with the atmosphere has been longer here than in the waters further offshore. Obviously, Heat Storage possesses an inherent temporal property; i.e., the longer the interaction between the (ice-free) water surface and the warming atmosphere, generally the higher the Heat Storage. Notice that heat transport from the atmosphere to the ocean is impeded when the ocean is covered by sea ice, the latter being an effective insulator.

The spatial distribution of the salinity depletion is not as well defined as that of the Heat Storage, though the highest values do appear to occur in the region off the Larsen shelf (Fig. 2). On the Larsen shelf markedly low salinity depletions are found, with the exception of station 73. This station lies close to the coastline, which hints that the high salt reduction is not caused by melting of sea ice, but by glacial meltwater from the abutting ice shelf. In the central Weddell Sea some stations display high salinity depletions as well. Since salinity depletion is due to the melting of sea ice (making it an apparent depletion), this implies that most sea ice was melted in the offshore Larsen region. Melting of sea ice consumes energy that consequently cannot be transferred into the water column; thus in the area where the salinity depletion is relatively large, a relatively small Heat Storage is anticipated, which is in accordance with the data in the offshore Larsen area (Fig. 2). Hence, since the amount of melted ice is inversely related to the time period the water was ice-free, there is good reason to believe that in the offshore Larsen region, the period the water has been ice-free was relatively short in comparison with the central Weddell Sea and the Joinville area.

Regional differences based on Heat Storage

Depletions of TCO_2, nitrate, phosphate and silicate are plotted as a function of Heat Storage in Fig. 3. In almost all diagrams a tendency of higher Heat Storage corresponding to larger depletions can be discerned. In Fig. 3 the data are further subdivided according to the different

Fig. 3 TCO_2 depletion (**A**), nitrate depletion (**B**), phosphate depletion (**C**) and silicate depletion (**D**) versus Heat Storage for all stations in the Weddell Sea, subdivided according to regions (see text). The lines were drawn by hand to enhance the trends. MJ is 10^6 joule



regions they originate from. The regions were chosen as based on the specific geographical location of the stations (for example, the Larsen shelf, stations 73–76; see Fig. 1), as well as on their characteristics with respect to Heat Storage (see Fig. 2). Hence, we distinguish the coastal area off Joinville Island (stations 69–62) as an area of enhanced Heat Storage, the offshore Larsen area (stations 79–88) with low Heat Storage and high salinity depletion and, finally, the central Weddell Sea (stations 36–61). An elaborated comparison of chemical (nutrient availabilities), physical (temperature and salinity) and biological (phytoplankton species) parameters by Semeneh (1997) and Semeneh et al. (1998) supports this selection of different regions. Pronounced differences in the mean depletions of most properties for the four regions are revealed in Table 1. For almost all properties the depletions attain the highest values, and are on average the highest, on the Larsen shelf. The mean nitrate depletion on the Larsen shelf is much higher than that in the Weddell Sea marginal ice zone in any season (see Goeyens et al. 1995). Areas with enhanced depletions include the region off Joinville Island and the offshore Larsen area. In the central Weddell Sea depletions are markedly low, and only comparable to early season conditions in the marginal ice zone (Goeyens et al. 1995).

The magnitude of a depletion depends both on the property concentration difference of the temperature-minimum layer and the surface layer, and the temperature-minimum depth (see equations 1, 2). Table 1 shows that regional trends in depletions can also be distinguished in the property concentration differences. There is also a regional variation of the temperature-minimum depth, which particularly elevates the depletion level on the Larsen shelf as compared to the other regions. Differences between the central Weddell Sea and the other regions are, however, clearly due to property concentration differences, rather than to a variation of temperature-minimum depth.

Figure 3 shows that the anticipated relationships between Heat Storage and the property depletions are strikingly different for the different regions, where the difference between the offshore Larsen area and the central Weddell Sea is especially remarkable. Off Joinville the depletion level does not change much with Heat Storage. For silicate depletion, the observations generally show a different picture than for the other nutrients and TCO_2. These results are intriguing in several aspects. A close correlation between Heat Storage and nutrient depletions (Fig. 3) is not obvious. The fact that the increase of the surface layer temperature in Antarctic waters would play some role in the onset of phytoplankton growth is not surprising (Tilzer et al. 1986). However, that nutrient consumption and thus phytoplankton production would be higher the more heat is contained in the surface layer suggests that heat is instrumental for the progress of a phytoplankton bloom. Although it cannot be ruled out that heat plays some part in this, the correlation of Heat Storage and nutrient depletions could also imply a third common factor. This common factor is probably the time period of light availability, that is, starting from the moment the water is ice-free. As already discussed, Heat Storage has some relation to time. While for Heat Storage the time period the water has been ice-free is an essential condition, this time period is also characterized by abundant light availability in the surface layer. As regards the removal of nutrients, it is obvious that the longer the period of light availability, the more nutrients will be utilized by photosynthesis.

We should also consider the occurrence of algae in the sea ice, which might have consumed nutrients before the ice-free period. As the extrapolated relationships of Heat Storage and the depletions for most regions tend to go through the origin (Fig. 3), the contribution of "ice algae" is probably small, as earlier suggested by Goeyens et al. (1995), who found a negligible contribution of nutrients in the ice to the water column. The only exception is the area off Joinville Island, which may have positive depletions at zero Heat Storage (Fig. 3). Although most water column algae could also occur in the sea ice (Smith and Sakshaug 1990), some species known as prominent ice inhabitants were found in relatively high numbers at Joinville stations, including

Table 1 Average depletions of several properties for four different regions in the Weddell Sea. Also given is the corresponding difference in property concentration between the temperature minimum layer and the summer surface layer for these different regions. Stations composing a particular region are given with the description of the region. For station positions refer to Fig. 1

	Offshore Larsen (79–88)	Larsen shelf (73–76)	Off Joinville (62–69)	Central Weddell (36–61)
TCO_2 depletion (mmol m^{-2})	1629.9	4551.0	2670.2	636.5
TCO_2 diff. (μmol kg^{-1})	29.4	41.8	33.5	8.5
Nitrate depletion (mmol m^{-2})	263.9	740.4	384.1	84.3
Nitrate diff. (μmol kg^{-1})	4.7	6.8	5.1	1.1
Phosphate depl. (mmol m^{-2})	22.8	44.9	24.7	7.2
Phosphate diff. (μmol kg^{-1})	0.41	0.41	0.30	0.10
Silicate depl. (mmol m^{-2})	479.4	522.1	398.6	124.2
Silicate diff. (μmol kg^{-1})	8.8	4.9	4.7	1.6
Salinity depletion (g m^{-2})	24.9	15.5	15.0	17.0
Salinity diff.	0.45	0.14	0.20	0.24
Heat Storage (MJ m^{-2})	56.3	337.4	361.1	101.4
Temperature diff. (°C)	0.26	0.78	1.05	0.35
Temp. minimum depth (m)	55	104	83	72
Temp. minimum range (m)	(50–75)	(100–115)	(50–125)	(50–100)

Haslea spp., *Nitzschia cylindrus*, *N. linolea* and *N. prolongatoidus* (Semeneh et al. 1998). This would support a possible contribution of "ice algae" to the nutrient consumption in the area off Joinville Island.

This interpretation of the relationship between Heat Storage and nutrient depletions presumes phytoplankton photosynthesis to be the cause of the nutrient depletions. We may seek validation for this assumption by checking the proportions between the nutrient depletions. In Table 2 the ratios of depletions are given for all combinations of properties as the mean of *all* stations. The mean nitrate to phosphate depletion and the TCO_2 to nitrate and the TCO_2 to phosphate ratios have the smallest coefficients of variation (CV). All other ratios have CVs (partly far) over 50%, being indicative of very large (spatial) spreading. The ratios involving TCO_2, nitrate and phosphate among themselves are not different from the Redfield stoichiometry (see also Hoppema and Goeyens 1999), which describes the relative variations of these compounds due to photosynthetic activity. If our calculated ratios deviate much from the Redfield ratios, this would be an indication that advection may be important in determining the depletions.

In Fig. 3 it should be noted that in the offshore Larsen area a relatively high level of depletions has been reached at very low Heat Storage, i.e., in a relatively short period of time. Notably, the depletions of TCO_2, nitrate and phosphate are about 5–7 times larger per unit Heat Storage in the offshore Larsen area than in the central Weddell Sea. This means that phytoplankton productivity (rate of production) is much higher in the former area than in the latter. On the Larsen shelf, higher depletions were found than in the offshore Larsen area, but these were (as based on the high Heat Storage) probably produced over a longer time period.

Ratios involving silicate depletion have very large CVs (Table 2), indicating a large spatial variation of silicate depletion. The reason is that silicate is not utilized by all phytoplankton species. Since the share of diatoms to the whole phytoplankton population is highly variable for different areas (as also observed during our cruise; Semeneh et al. 1998), the silicate consumption in comparison with other nutrient consumptions is variable too. In contrast with the other nutrient depletions, the silicate depletion has an explicit relationship with Heat Storage only in the offshore Larsen area (Fig. 3D). Moreover, among the highest silicate depletions were observed in the offshore Larsen area. These observations are indicative of a sizable contribution of silicate-consuming diatoms to the total phytoplankton production in this area. Phytoplankton counts confirm that the highest diatom biomass is indeed found in the offshore Larsen area (and on the Larsen shelf), and furthermore show that the percentage of diatoms to the total phytoplankton population is high, amounting to about 50 (Semeneh et al. 1998). These results allow an additional conclusion for the following reason: depletions yield an average of the whole summer season until the moment of sampling, whereas phytoplankton counts depict only the situation at the moment of sampling. The fact that both kinds of observations are in good agreement for the offshore Larsen area strongly suggests that phytoplankton was actively growing, the bloom being in its early stages. This in turn is in keeping with the very high specific nitrate uptake rate in the offshore Larsen area (Semeneh et al. 1998). Goeyens et al. (1995) demonstrated that relatively high specific nitrate uptake rates prevail in the beginning of the productive period.

A plot of the specific silicate depletion versus the specific nitrate depletion (Fig. 4) demonstrates that specific depletion ratios in the central Weddell Sea and the offshore Larsen region are close to 1; this means that removal of these nutrients is proportional to the respective nutrient availabilities. Specific depletion is the depletion normalized to its corresponding winter concentration; specific silicate to nitrate depletion ratios > 1 indicate potential nitrate excess, whereas ratios < 1 indicate potential silicate excess (Goeyens et al. 1998). Generally, when the specific silicate to nitrate depletion ratios are proportional on a 1:1 basis (as in the central Weddell Sea and offshore Larsen areas), this refers to phytoplankton communities in which both diatoms and non-silicate-consuming species are prevalent. In contrast

Table 2 Mean ratios of all combinations of parameter depletions. For each station the ratio was calculated and the all-station mean with the standard deviation is given; the coefficient of variation (standard deviation as percentage of the mean) is given in parentheses. The ratios should be read as the parameter in the first column divided by the parameter in the first row

	Nitrate	Silicate	Phosphate
TCO_2	7.0 ± 2.3 (33%)	6.4 ± 5.6 (88%)	86 ± 24 (27%)
Nitrate		1.0 ± 1.1 (114%)	12.7 ± 2.9 (23%)
Silicate			17.6 ± 10.6 (60%)

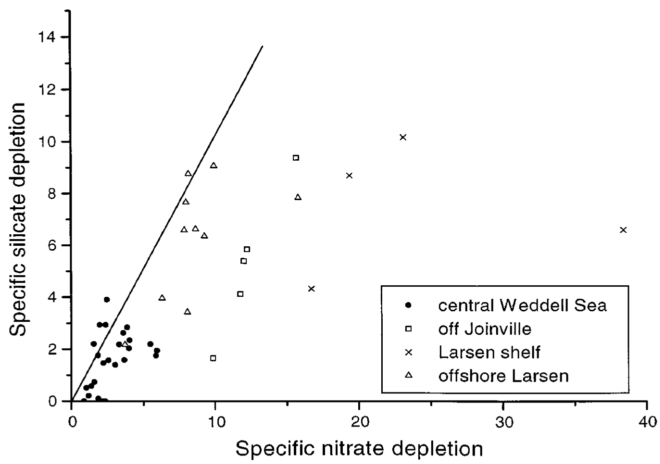


Fig. 4 Specific silicate depletion versus specific nitrate depletion, subdivided according to regions (see text). The specific depletion is the depletion (mmol m^{-2}) divided by the corresponding concentration (µmol kg^{-1}) in the temperature-minimum layer (i.e. the winter concentration). The line drawn displays the 1:1 proportionality

to the central Weddell Sea and offshore Larsen regions, the Larsen shelf and the off-Joinville regions adhere to silicate excess characteristics with specific depletion ratios < 1. Such ecosystems are known to display elevated nitrate uptake rates during the earliest phase of the productive season (Goeyens et al. 1998) and possible predominance of non-diatoms (e.g. *Phaeocystis antarctica* was very abundant at station 63).

Scenario for intense nutrient removal

What could be the reason for the offshore Larsen area to be the ideal locus for plankton growth and nutrient removal? Elevated silicate depletions and diatom biomass attest to beneficial conditions as opposed to the central Weddell Sea. The silicate depletions in the offshore Larsen area are even higher than those on the Larsen shelf and off Joinville Island, both of which are coastal areas that are known to support enhanced primary production (von Bodungen et al. 1986; Karl et al. 1991). We surmise that, given the early stage of the bloom in the offshore Larsen area, the nutrient depletions had not even reached their seasonal maximum at the time of sampling. Additionally, other phytoplankton species contributed significantly to the extent of nutrient removal and primary production. Enhanced nitrate depletions and high nitrate uptake rates were observed in diatom-rich, as well as *Phaeocystis*-rich, phytoplankton communities of the Ross Sea during the earliest phases of the growth season (Goeyens et al., in press). Therefore, there is good reason to believe that the status of the ecosystem off Larsen Shelf is biologically healthy and productive with an elevated advantageous biodiversity compared to adjacent regions.

An essential requirement for a phytoplankton bloom to develop is that the surface water column has a high stability for a sufficiently long period of time. Indeed, a study on the western side of the Antarctic Peninsula by von Bodungen et al. (1986) concludes that the hydrography-topography interaction is the most important factor for the onset of a phytoplankton bloom. Including arguments based on Heat Storage we present the following scenario for bloom development in the offshore Larsen area, as compared to the central Weddell Sea. In the offshore Larsen area the time period that the water has been ice-free is relatively short. It is important to appreciate that this area is usually characterized by perennial ice cover. From observations with drifting buoys in the Weddell Sea we know that the summer surface layer began to be shaped in approximately October 1992, as revealed by a rise of the temperature (Sellmann and Kottmeier 1993). This renders (parts of) the central Weddell Sea ice-free for about 2–3 months until sampling. Total Heat Storage into the surface layer of the central Weddell Sea (Fig. 2) thus occurred over a relatively long period of time, whereas for the offshore Larsen area the Heat Storage per time period was larger. We can think of this as if, in the offshore Larsen area, an uninterrupted period of calm weather has been prevalent in which a stable surface layer could be formed, whereas in the central Weddell Sea alternating periods of calm and stormy weather occurred, preventing a stable surface layer being shaped for a long enough period for a bloom to develop. The sheltering effect of the Antarctic Peninsula to the west and the high extent of ice cover in the contiguous areas are other factors that reduce the effects of possible storms particularly in the offshore Larsen area. Additional support comes from our observations that the temperature minimum occurred at a somewhat shallower depth in the offshore Larsen area than in the central Weddell Sea.

Though water column stability is a prerequisite for the development of a phytoplankton bloom, the final extent of the bloom will depend on additional factors. Two factors may particularly promote the magnitude of the phytoplankton bloom in the offshore Larsen area. First, there is the physiological adaptation of the phytoplankton. In the marginal ice zone of the Antarctic, the pelagic phytoplankton should meet the requirements posed by the ice cover, which causes extremely adverse light conditions for a considerable part of the year; after the melting of the ice the phytoplankton is exposed to ambient light for only a relatively short period. For the offshore Larsen area this holds in an extreme way, as the ice cover remains in place during most of the year. Hence, the local phytoplankton population is probably extremely well adapted to the inferior light regime, enabling it to grow rapidly during a short time period (which is in line with the very high specific nitrate uptake rate found in this area). Second, there is the reduced importance of top-down control. The structure of Antarctic ecosystems is strongly determined by zooplankton grazers, of which krill (*Euphausia superba*) is the most important (Smetacek et al. 1990). This holds especially for the marginal ice zone, where its life-cycle is closely coupled to the varying extent of ice coverage (Tréguer and Jacques 1992). They are the agents that end phytoplankton blooms and keep phytoplankton standing stocks low. In the offshore Larsen area the ice cover is extensive and in many years the ice does not open at all. Hence, there is no permanent large phytoplankton population present. It is not effective for grazers to be present in such a barren area, and thus the role of grazers is not expected to be important here. This, in turn, gives rise to rapid and extensive phytoplankton blooms, if physical conditions (melting of the sea ice) allow.

Estimation of primary productivity

If the time frame in which depletions have occurred is known, primary productivity can be estimated. Observations with drifting buoys in the Weddell Sea revealed that air and sea surface temperatures rose precipitously in the beginning of October 1992 (Sellmann and Kottmeier 1993). Thus, at the time of sampling, the second half of December 1992 and the first half of January 1993, the summer surface layer had an age of 2–3 months. This time frame is confirmed by Nelson et al. (1987), who suggested that seasonal phytoplankton growth starts as early as October in the Weddell Sea. This age is pertinent to the central Weddell Sea and the near-coastal areas (Larsen shelf and off Joinville Island; these areas were open early in the season because of coastal polynyas). As already mentioned, the offshore Larsen area had been ice-free for a shorter period. We assign a typical time frame of 15–30 days for that area. With these different time frames, primary productivity was calculated from the TCO_2 depletions, the results of which are presented in Table 3. Using TCO_2 depletions for this calculation has the advantage that primary productivity can be determined without applying approximative factors for the conversion of nutrient uptake into carbon fixation. CO_2 uptake from the atmosphere could affect the estimation, because the partial pressure of CO_2 in the surface layer is considerably reduced through the uptake of CO_2 by phytoplankton (Hoppema et al. 1995). However, the effect of air-sea exchange of CO_2 is smaller than 10% (Hoppema and Goeyens 1999) and consequently productivity is only a little underestimated due to this effect.

The productivity data in Table 3 confirm the pronounced spatial variability that was described earlier, the mean values ranging between 85 and 1139 mg C m^{-2} day^{-1}. In the central Weddell Sea, productivity is very low at about 100 mg C m^{-2} day^{-1}, while the coastal areas (Larsen shelf and off Joinville) show distinctly elevated productivities. The highest mean productivity was found in the offshore Larsen area, though the highest value for an individual station, amounting to 1000–1500 mg C m^{-2} day^{-1}, was found at station 73 on the Larsen shelf. This peak productivity is presumably promoted through continual stabilization of the upper water column through glacial meltwater of the abutting ice shelf and optimal sheltering close to the coastline. Possibly the bloom at station 73 was also formed under the influence of ice platelets ("underwater ice"), which provide ideal conditions for (super)blooms near ice shelves (Smetacek et al. 1992).

Table 3 Primary productivity estimates calculated from TCO_2 depletions (see Table 1) for different regions in the Weddell Sea. Estimates appear for assumed time intervals of 60 and 90 days, except for the offshore Larsen region, where these are 15 and 30 days

	Primary productivity (mg C m^{-2} day^{-1})		
	60 days	90 days	
Larsen shelf	911	607	(n = 4)
(Coastline station 73)	1498	998	
Off Joinville	534	356	(n = 5)
Central Weddell	127	85	(n = 24)
	15 days	30 days	
Offshore Larsen	1139	570	(n = 7)

The present primary productivity estimate for the central Weddell Sea is in agreement with current mean estimates for the open ocean of the Antarctic, amounting to 100–300 mg C m^{-2} day^{-1} (Jacques 1989; Smith and Sakshaug 1990). Our central Weddell Sea value also agrees well with the estimates of Rubin et al. (1998), obtained for the offshore Ross and Amundsen Seas with their depletion method. However, our data stand in contrast with those of Jennings et al. (1984), who found (at least) 2–4 times higher values for the central Weddell Gyre near the prime meridian. It is not clear to us what causes this substantial difference between these comparable regions, the productivity estimates being obtained with similar methods. It should be noted that the value of Jennings et al. (1984) is based on one single station, while we use data of a whole transect. Part of the discrepancy may be due to interannual variability and/or differences in seasonal maturity.

Coastal and shelf areas are known regions of elevated productivity in comparison with the open ocean, which is well illustrated by a comprehensive comparison by Mathot et al. (1992). Our productivity estimates for the Larsen shelf and the coastal areas off Joinville and off the Larsen shelf fit in this picture. It is clear, however, that our area of investigation is not outstanding with regard to its primary productivity, as much higher values were reported for other Antarctic shelf regions. Our productivity estimates for the eastern side of the Antarctic Peninsula are in good agreement with data from the western, Pacific side of the Peninsula, where typical values of 800–1000 mg C m^{-2} day^{-1} were measured using isotope techniques (von Bodungen et al. 1986; Holm-Hansen and Mitchell 1991) and with the eastern Weddell Sea coastal area (von Bröckel 1985).

Conclusions

The positive, clear-cut relationships between Heat Storage and nutrient depletions suggest that a high rate of heat transport into the surface layer has a positive effect on the development of phytoplankton blooms. It should be added that this will always be in combination with sufficient stability of the surface layer. In the offshore Larsen area, and also on the Larsen shelf, surface layer stability is brought about by calm weather in the summer and the sheltering effect against storms through the nearby continent. In the investigated area east of the Larsen Ice Shelf this leads to very high phytoplankton growth rates and biomass.

It is important to appreciate that the depletions and productivities we found in the area off the Larsen Ice Shelf are large, but not larger than in comparable coastal areas of the Antarctic. Smetacek et al. (1992) speculated that off the Larsen Ice Shelf superblooms could occur, which are associated with platelet ice that forms near ice shelves. In the superbloom they observed, phytoplankton growth was limited by nitrogen availability, a condition seldom found in Antarctic waters. In our data set, station 73, closest to the Larsen Ice Shelf, was characterized by the largest depletions. However, the nutrient concentrations were sufficiently high that any limitation is unlikely. This station may well be the remnant of a superbloom, which was dispersed on the shelf and/or advected to the north along the coastline.

We conclude that the parameter Heat Storage (in combination with the apparent salinity depletion) is a useful property for unveiling the physical history behind nutrient depletions. Heat Storage has a close relationship with light availability, which in Antarctic waters is a factor of utmost importance.

Notwithstanding the (advantageous) property of depletions giving a spatially integrated picture of nutrient removal, a distinct spatial variation of the depletions themselves can be discerned in our data. This variability is associated with different physical regimes. Hence, though depletions possess an inherent property for integrating, the specific physical conditions in a region should always be accounted for.

The primary productivity calculated from our depletion data seems to fit well into the range of estimates of productivity based on isotope incubations. This suggests that there is no reason to suppose a discrepancy between these two methods for determining primary productivity.

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