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Winter production of sea ice algae in the western Weddell Sea

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Abstract

Short- and long-term series of observations were carried out during the US-Russian Ice Station Weddell no. 1 (ISW-1) Expedition, 1992, in the western Weddell Sea. The goal of in situ observations was to assess the winter biological dynamics within the 1-year and newly formed sea ice. It was shown that at the initial stage of ice formation, there is a period of mechanical harvesting of plankton cells from the sea water. In this period, the biomass of ice algae was 10-20 times lower, in terms of chlorophyll *a* concentration, than that of the underlying phytoplankton. A remarkable increase in chlorophyll *a* content begins when the ice is 30-40-cm thick and environmental conditions are more favourable for algal growth. As a rule, reproduction of algae in the newly formed ice takes place within the lower layer of ice and close to the skeletal layer, where sea water with high nutrient concentrations is transported to the cells through brine channels during oscillation processes. By contrast, the highest concentrations of chlorophyll *a* in the 1-year ice were found within the upper layers. It was shown that chlorophyll *a* concentrations produced by the sea ice algae within both the young and the 1-year sea ice were always remarkably higher than chlorophyll *a* concentrations in the sea water below the ice. These results also indicate that winter production by ice algae in the extensive Antarctic sea ice zone should be considered an important factor in future biological models of the Southern Ocean.

Resume

Des series d'observations a court et a long termes ont ete effectuees en 1992 en Mer de Weddell occidentale, a 1'occasion de la premiere expedition americano-russe 'Ice Station Weddell' (ISW-l). Le but de ces observations in situ etait d'evaluer la dynamique biologique au sein de la glace de premiere annee et de la glace nouvellement formee. II a ete montre que, aux premiers stades de formation de la glace, il existe une periode de collecte mecanique des cellules phytoplanctoniques a partir de 1'eau de mer. Pendant cette periode, la biomasse algale etait 10 a 20 fois plus faible, en termes de concentration de chlorophylle *a,* au sein de la glace que dans la colonne d'eau sous-jacente. Une augmentation remarquable de la teneur en chlorophylle *a* debute quand la glace atteint une epaisseur de 30 a 40 cm et que les conditions ambiantes sont favorables a la croissance algale. En regie generate, la croissance des algues intervient, dans la couche inferieure de la glace nouvellement formee, a proximite de la couche de cristaux non consolides, ou de 1'eau de mer riche en sels nuritifs est apportee aux cellules par les canaux a saumure au cours du processus d'oscillation. Dans la glace de premiere annee, en revanche, les plus fortes concentrations de chlorophylle *a* ont ete observees dans les couches superieures. II a ete montre que les concentrations de chlorophylle *a* produites par les algues de glace, aussi bien dans la glace nouvellement formee que dans la glace de

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premiere annee, sont remarquablement plus elevees que dans la colonne d'eau sous-jacente. Ces resultats suggerent que la production hivemale des algues de glace dans la vaste zone couverte par la banquise antarctique doit etre serieusement prise en compte dans les future modeles biologiques de 1'Ocean Austral.

Keywords: winter production; Sea ice algae; Weddell Sea

1. Introduction

Sea ice is an important component of the Antarctic marine ecosystem. Every austral winter, an ice cover of 16 X 106 km2 forms over previously open waters in the Southern Ocean (Zwally et al., 1983). Around most of the Antarctic continent, the ice edge retreats to the coast in summer, except in the western Weddell Sea and the Bellingshausen-Amundsen Seas.

Our knowledge of the Antarctic biological production has so far been based mainly on the summer observations in the ice-free ocean and on the study of the seasonal ice formed in winter around the continent, most often from observations in coastal regions (e.g., Meguro, 1962; Bunt, 1963; Burkholder and Mandelli, 1965; Andriyashev, 1967; Hoshiai, 1977). It was shown that the young ice, formed in winter in the area of open water, concentrates algal cells from the underlying water and that the initial chlorophyll *a* concentrations are higher within the ice than in the water (Clarke and Ackley, 1984). This mechanical concentration of cells is further enhanced by subsequent reproduction of ice algae. It has also been noticed that pelagic ice chlorophyll *a* concentrations in the eastern Weddell Sea, ranging from 0.1

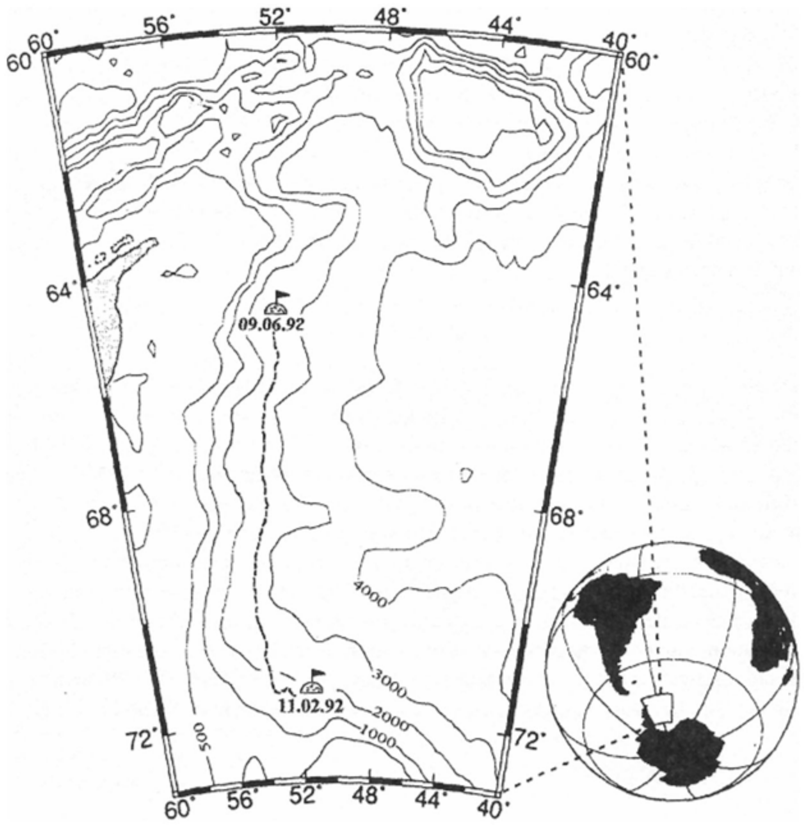

Fig. 1. Track of the US-Russian ISW-1 in the western Weddell Sea, February-June 1992.

to 3.8 |xg 1 ', are significantly lower than the values (300-2000 (Jig I"1) found in Antarctic coastal regions (Sullivan and Palmisano, 1981).

The biology of ice-covered seas is of special interest because of the large extent of ice cover during the whole year. However, little is known about ecologically important questions, such as sea ice biological production, colonisation by microbiota, community organisation, spatial and temporal patterns during winter sea ice development. However, understanding is needed of how sea ice and winter ice dynamics influence community structure, the nature and rates of biotic processes at the initial stages of the ice formation and continued growth in the Antarctic sea ice zone.

The main goal of the present study was to examine the evolution of sea ice algae communities and features of biotic processes during the early austral winter, characterized by decreasing incident light, snow accumulation and low air temperature. This paper presents two series of data obtained during the US-Russia Ice Station Weddell no. 1 (ISW-1) Expedition (Gordon and Lukin, 1992). Observations were carried out in the pack ice area of the western Weddell Sea, where ISW-1 drifted between 72° and 65°S, and 51° and 53°W, from 11 February to 9 June 1992 (Fig. 1).

2. Materials and methods

The sampling strategy was based on the short- and long-term observations of salinity, silicate and chlorophyll *a* concentrations as well as the development of sea ice algae during the ice formation and its continued growth (Melnikov, 1995). Short-term series were conducted in the area of newly formed ice off the ice floe on which ISW-1 was located. Long-term observations were carried out in the area of the 1-year ice floe with a thickness of 1-1.5 m and a snow cover of about 30-40 cm.

Short-term observations included: (1) 24-h series on a lead with newly formed sea ice at 4-h sampling intervals (20 May), and (2) 8-day series on the same lead with one sample collection per day (21-28 May). Long-term observations were conducted: (1) on the lead with young growing sea ice (18 March-7 June), and (2) on the 1-year ice floe (29 February-27 May).

All ice core samples were taken with an ice coring auger 10 cm in diameter. The total ice core length was measured, a surface was cleaned and the whole ice core was divided into a number of equal parts depending on the total length. The actual number of sections was determined in each case by a trade-off between the need for a sufficient sample

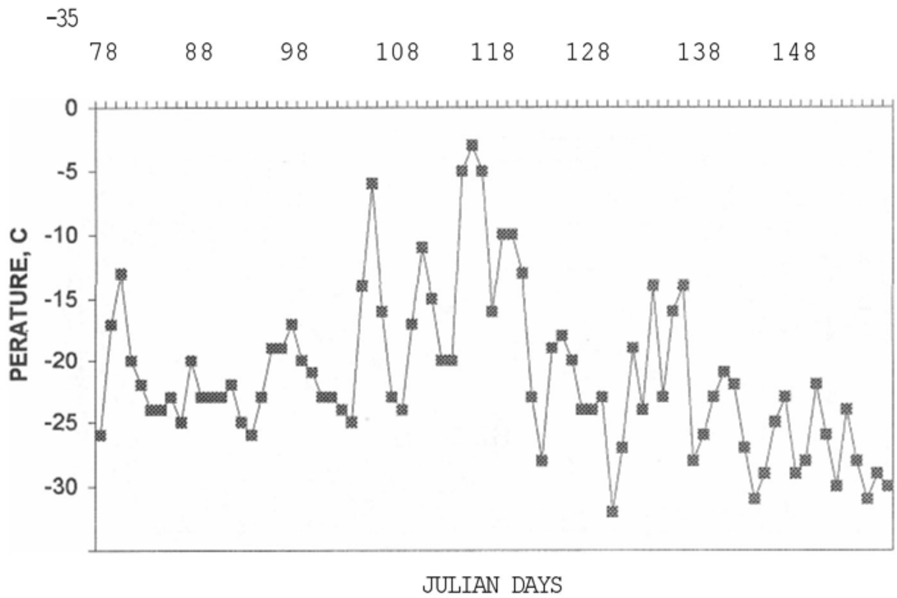

Fig. 2. Daily sea ice surface temperature (°C) during the period of observations (March-June 1992).

volume for the analyses, and the adequate representation of physical, chemical and biological features and their variations both within the sea ice and at the snow–ice and ice–water boundaries, i.e., within the upper, middle and bottom layers. Every ice section was crushed into small pieces, put into 3–4 l plastic bottles, then melted at room temperature.

Information on the sea water in contact with the underside of the sea ice was obtained from samples collected with 2-l plastic syringes by SCUBA divers. Dives were carried out through a separate hydrohole made in the ice floe. Some of the observations were carried out under the newly formed ice in the lead. Samples to determine phytoplankton composition were collected every 10 days by pumping 50 l of the surface sea water from the ice hole to a plastic tank. Phytoplankton were concentrated to 50 ml using a reverse filtering system with a 10-μm mesh nylon filter. The samples were fixed with 4% formal-dehyde.

Samples of the ice-melt water, as well as the sea water samples, were tested for the following: salinity with a Beckman salinometer, silicate after Mullin and Riley (Strickland and Parsons, 1968); chlorophyll *a* concentration according to Scientific Committee on Oceanic Research-UNESCO (1966). Both sea ice biota and plankton collections were processed by methods used in planktonology (Kisilev, 1969).

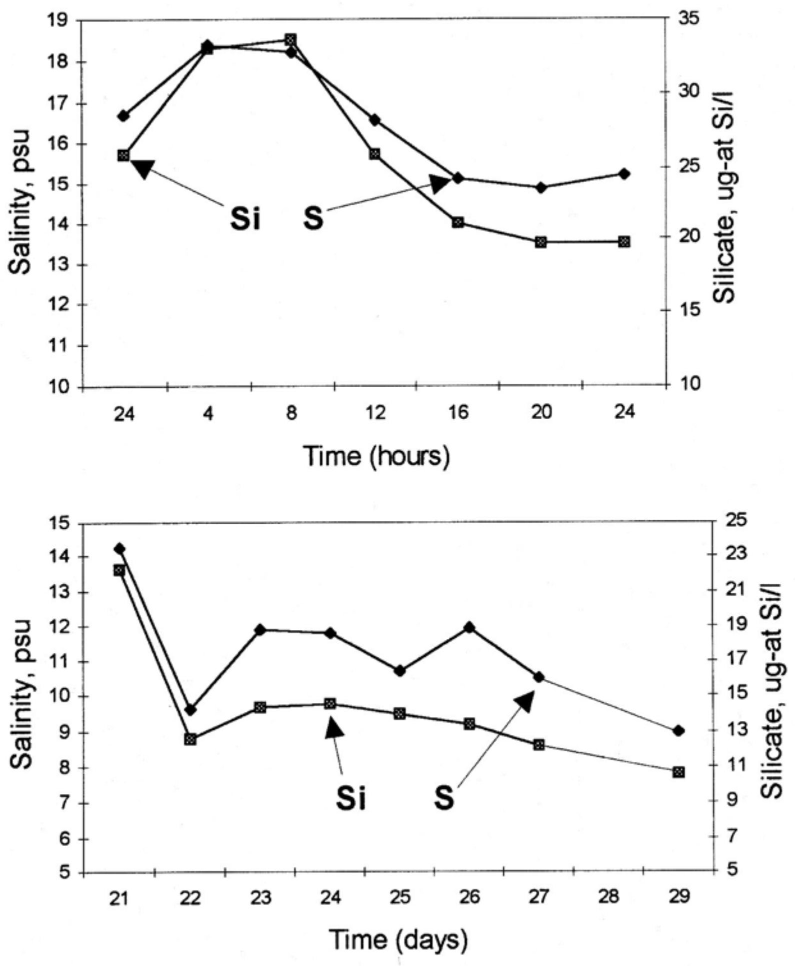

Fig. 3. Variations of salinity (S) and silicate (Si) in the newly formed young ice during the 24-h (20–21 May 1992, top diagram) and the 8-day (21–28 May 1992, bottom diagram) series of observations.

Diatom enumeration and species identification were performed using a Zeiss inverted light microscope under laboratory conditions.

3. Results

3.1. Oceanography and ice conditions

The observations were carried out within the western Weddell boundary current flowing northward over the continental slope. The vertical structure of the under-ice water column was characterised by nearly isothermal conditions in the upper 30 m and a weak seasonal pycnocline at 35–50 m mostly due to salinity changes in the range of ca. 34.15–34.45 psu in summer (Gordon and Huber, 1992).

The ice field where ISW-1 was established was consolidated from small ice floes, with many under-ice shelves, hummocks, caverns, cracks, etc. Its bottom surface was plain without platelet ice crystals. Salinity values measured at 0 m on SCUBA dives were as follows: 30.0 psu (29 February), 30.3 psu (7 March), 24.5 psu (11 March), 28.8 psu (15 March), 29.0 psu (24 March), 33.5 psu (23 April) and were

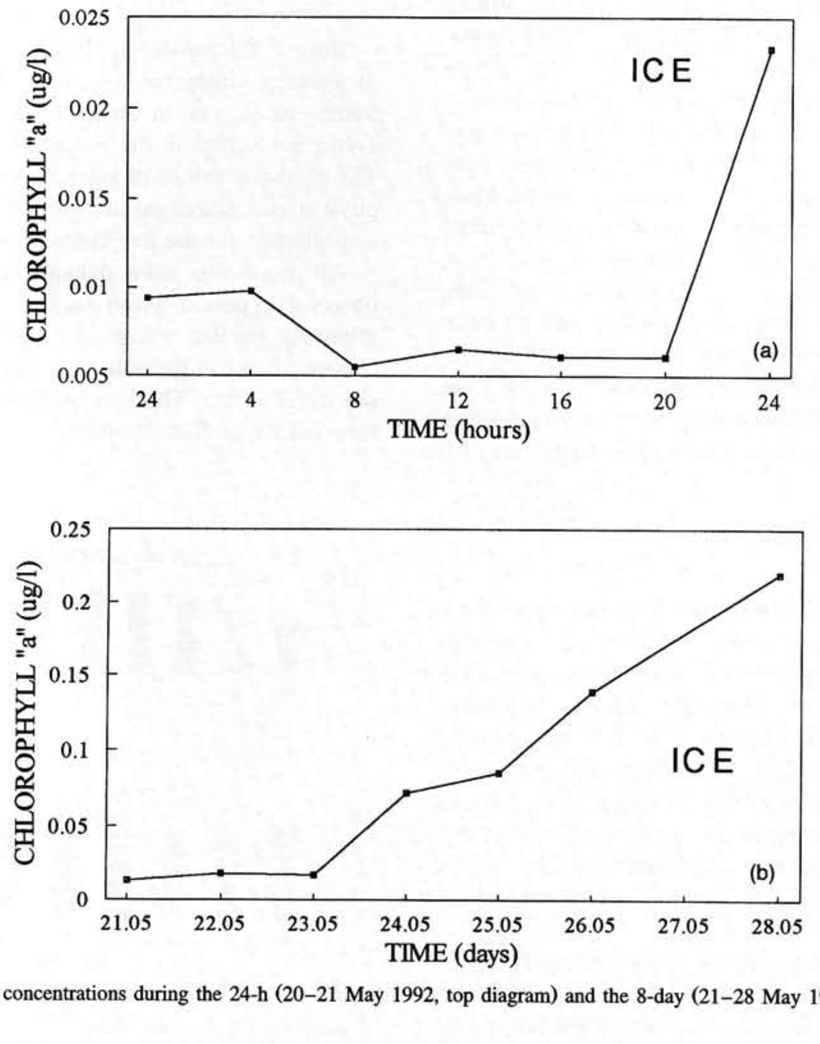

Fig. 4. Chlorophyll *a* concentrations during the 24-h (20–21 May 1992, top diagram) and the 8-day (21–28 May 1992, bottom diagram) series of observations.

remarkably lower than the CTD data for the mixed layer as shown above. There is little doubt that this was due to sea ice melting taking place throughout the period of observations. The latest value, on 23 April was, however, higher than the previous figures, indicating that the melting process was slowing down at that time. The end of melting by late April was confirmed by a considerable erosion of the seasonal pycnocline (Martinson et al., 1992).

The season of observations corresponds to the early austral winter as indicated by decreasing incident radiation, snow accumulation and low air temperature. The latter varied during the period of observations from -3 to $-33°C$ (Fig. 2). In the underlying sea water, temperature ranged from -1.85 to $-1.83°C$, salinity from 34.06 to 34.42 psu, silicate concentration from 71.4–51.8 $\mu mol\ l^{-1}$ and chlorophyll *a* from 0.47 to <0.01 $\mu g\ l^{-1}$. The phytoplankton in the surface sea water was very poor in diatoms, of which 18 species were found, with nine species, *Corethron criophilum*, *Fragilariopsis vanheurckii*, *F. cylindrus*, *F. separanta*, *F. curta*, *Manguinea rigida*, *Pinnularia quadratarea*, *Thalassionema nitzschioides*, and *Thalassiosira antarctica*, making up $>30\%$ of the total number of cells. Among them, *F. curta*, *F. cylindrus* and *C. criophilum* were dominant. In no water sample did chlorophyll *a* concentrations exceed 0.5 $\mu g\ l^{-1}$. In other words, they remained orders of magnitudes lower than the concentrations within the sea ice.

3.2. Short-term observations

During the 24 h of ice formation from open water to 9-cm thick, the processes of incorporation of both salts (in terms of salinity and silicate) and particulate matter (in terms of chlorophyll *a*) were nonlinear (Figs. 3 and 4). During the first 8 h (the greatest growth rate of the ice), the salinity and silicate sea ice concentrations increased to values of 19 psu and 40 $\mu mol\ l^{-1}$, respectively, and then rapidly decreased. This tendency continued and the values reached 7.8 psu and 13.6 $\mu mol\ l^{-1}$ on the 8th day of observation.

Early in the observations, high concentrations of chlorophyll *a* were not found in the ice, nor was there noticeable colonisation of newly formed ice by phytoplankton. Sea ice chlorophyll *a* concentrations (<0.01 $\mu g\ l^{-1}$, Fig. 4a) were also much lower than the concentration in the surface sea water (0.24 $\mu g\ l^{-1}$) from which the ice was formed. The chlorophyll *a* concentration increased from the 3rd day of observations onwards, and reached on day 8 a value close to that in the sea water (Fig. 4b). During the first day of ice formation, only single cells of *F. cylindrus*, which was common in phytoplankton, were seen in the ice. On day 8, except for *F. cylindrus*, the sea ice algal community was dominated by *Aulacosira* sp., *P. quadratarea*, *T. nitzschioides*, and *T. antarctica*, which were also common in the phytoplankton.

3.3. Long-term observations

During the period of observations, the thickness of growing young sea ice increased from 42 cm in March to 97 cm in June, while the thickness of 1-year ice varied in the range 93–120 cm (Fig. 5). The observed values of salinity, silicate, and chlorophyll *a* concentrations are plotted in Figs. 6 and 7, respectively, for the two types of ice.

All parameters show dynamic activity during the observation period. Mean values within all layers are relatively similar, except for higher chlorophyll *a* concentrations in the bottom layer of growing young sea ice (Fig. 6c). This can be explained by temperature conditions more favourable for reproduction than

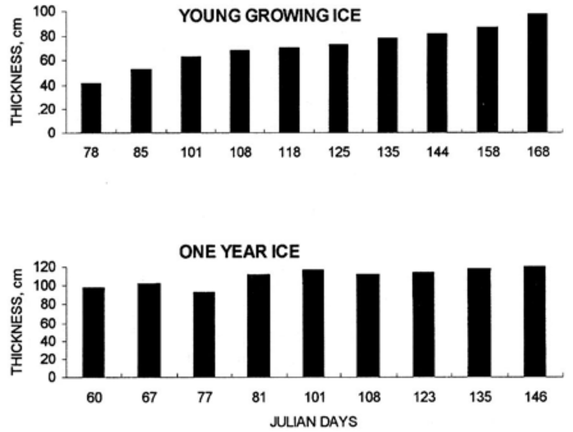

Fig. 5. Variations of sea ice thickness over the period of long-term observations (March–June 1992).

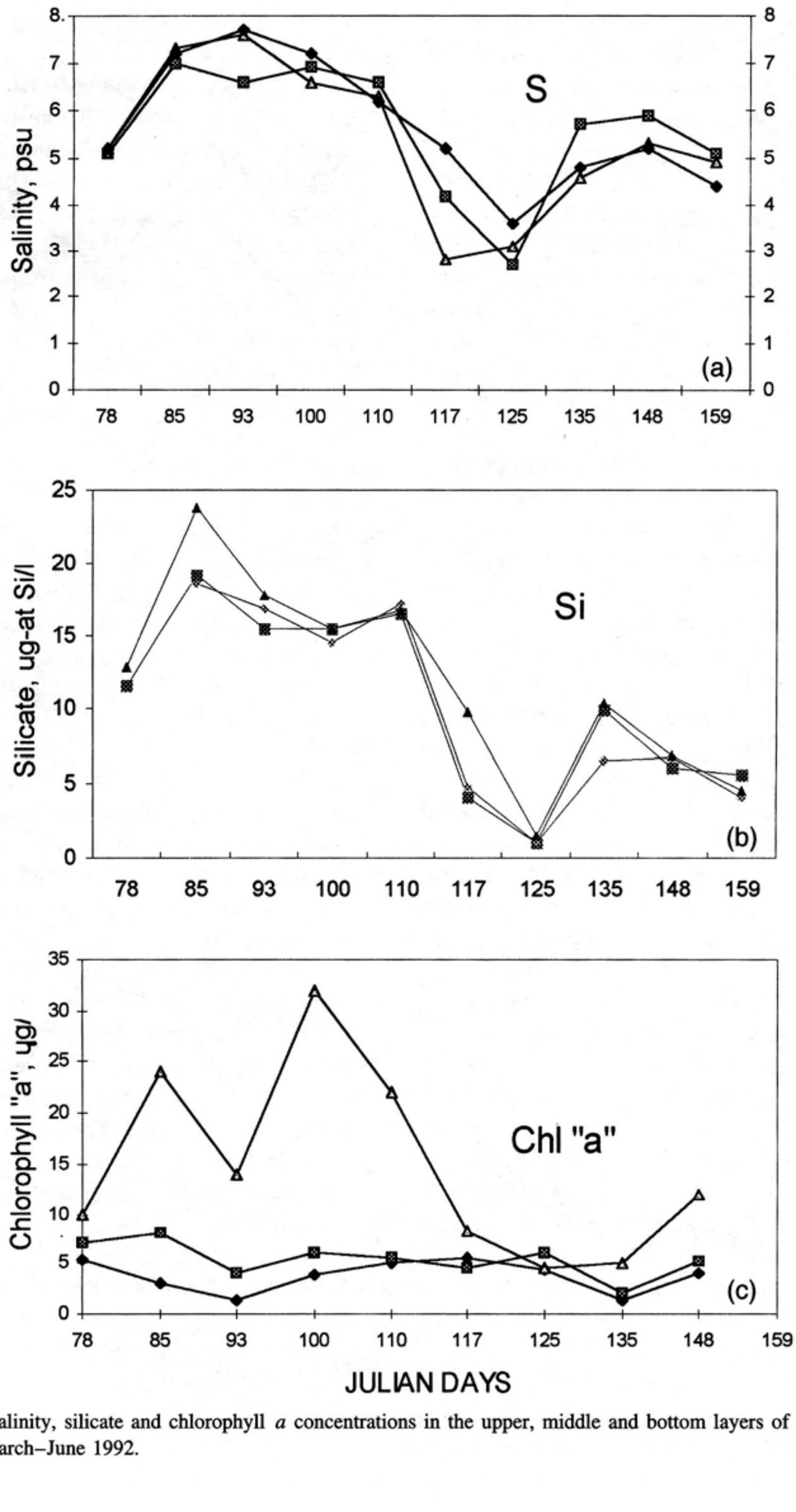

Fig. 6. Variations of salinity, silicate and chlorophyll *a* concentrations in the upper, middle and bottom layers of growing young sea ice formed on the lead, March–June 1992.

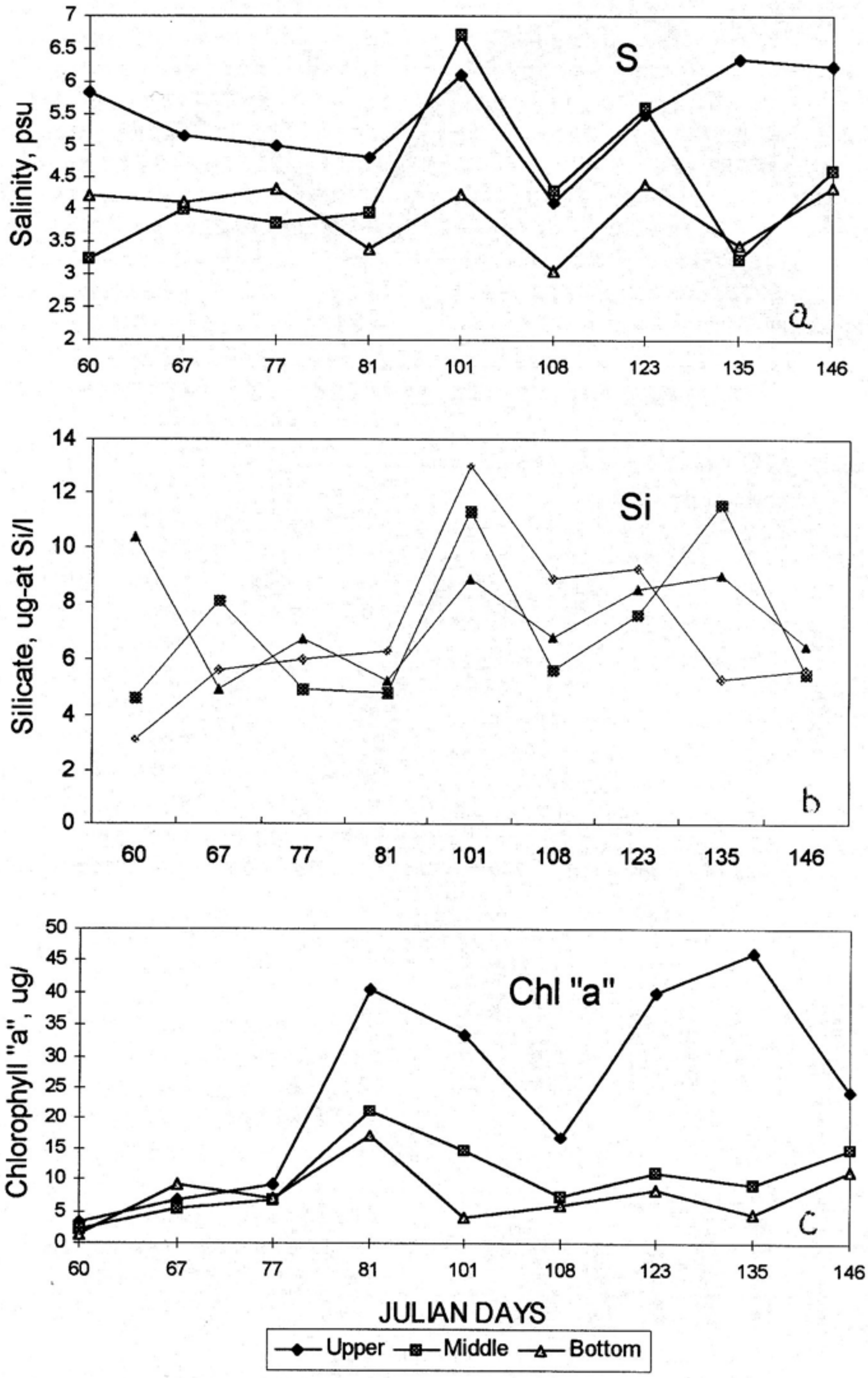

Fig. 7. Variations of salinity, silicate and chlorophyll *a* concentrations in the upper, middle and bottom layers of 1-year ice, March–June 1992.

those experienced by the algae in the middle and upper sections of the ice. The highest values of salinity (7-8 psu), silicate (17.9-24.3 (jimol T^{1}), and chlorophyll *a* (25-33 (jig I''^{1}) were measured during the period 85-110 Julian days, and the lowest (3-4 psu, 0.7-3.6 (jimol T^{1} and 5-6 fjig T^{1}, respectively) in the period 117-125 Julian days. During this period, the temperature of the ice surface increased from —25 to — 2°C and then rapidly decreased to - 33°C (Fig. 2). The higher values of all variables correspond to the colder days, and vice versa. The bottom layer of the young growing ice had the highest chlorophyll *a* concentrations (33 (jig I''^{1}), approximately an order of magnitude higher than in the upper layers (Fig. 6c). By contrast, the highest concentrations of chlorophyll *a* in the 1-year ice were found in the upper layer (46 (Jig I''^{1}) and the lowest in the middle and bottom layers (Fig. 7c).

The total list of sea ice algae identified in the growing young sea ice and in the 1-year ice consists of 96 and 93 species, respectively. On the basis of taxonomic analysis and relative abundance of diatom species within the ice, two types of sea ice communities were distinguished: (1) within the upper layer of the 1-year sea ice, and (2) within the bottom layer of the young growing sea ice.

The surface sea ice community of algae is developed within the upper layer of the 1-year ice, mainly in the boundary between snow and ice, an environment known as 'infiltration ice' (Buynitsky et al., 1973). The infiltration community consists mostly of large cells (9-30 (Jim), with *F. cylindrus* reaching up to 90% of the total cell number. The bottom sea ice community is developed close to the skeletal layer of the young growing ice. The species composition of this community is similar to that of the surface community of the 1-year ice, but there are considerable differences in the relative abundance of the various species. Thus, within the bottom layer, the contribution of *F. cylindrus* is sharply decreased, while the proportions of *C. criophilum, Nitzschia lecointei, N. helmii, F. antarctica, F. curia,* and the dinoflagellate *Prorocentrum antarctica,* are substantially increased. High chlorophyll *a* concentrations, in the range 20-50 |xg 1~', testify to very intensive biological processes within the thickness of both 1-year and young growing sea ice during the early austral winter.

4. Discussion

The phenomenon of sea ice algae development in the Antarctic sea ice zone is well known and widely discussed in the literature (e.g., Bunt and Wood, 1963; Meguro et al., 1967; Buynitsky et al., 1973; Sullivan and Palmisano, 1981; Ackley et al., 1987; Hoshiai et al., 1989). The observations at ISW-1 have shown that the maximum number of diatoms and the highest chlorophyll *a* concentrations are found within the upper layer of the 1-year ice and within the lower layer of the young growing ice, respectively. The observed differences can be explained by the interplay of two environmental factors: snow accumulation on the upper ice surfaces, on the one hand, and temperature conditions on the other hand limited the development of sea ice algae. In the case of the 1-year ice, when the snow cover reaches a thickness of about 1 m, the ice sinks below sea level under the weight, and the diatoms begin to develop within the snow-ice boundary, where the temperature conditions are close to those in the sea water. This environment is called 'plankton ice' (Meguro et al., 1967) or 'infiltration ice' (Buynitsky et al., 1973), and characterized by a 'brown layer' coloured by the diatoms. By contrast, the young growing ice is covered mostly by a thin snow layer (about 10-cm thick) from March to June (personal unpublished data). In this case, the infiltration phenomenon does not take place, and the diatoms develop actively within the bottom layer, where temperature conditions are more favourable for algal growth than in the upper layers (Melnikov, 1995).

The results of both the short- and long-term observations have shown that during the austral winter, despite sub-zero temperatures and low light conditions, the sea ice algae continue to develop within the 1-year and the young growing sea ice. Their biomass (in terms of chlorophyll *a* concentration) is several orders of magnitude higher than that of the phytoplankton in the underlying sea water. Photosynthetic rate experiments with ice algae incubated for 24 h conducted at the same time during the ISW-1 drift (Sullivan et al., 1992; Fritsen et al., 1993) showed net fixation of ^{14}C and indicated, that ice algae are physiologically active in winter/This result is supported by the in situ changes of ajgal biomass, observed as an increase of chlorophyll i *a* concentrations. It should be noticed that the net increase in the biomass of ice algae is determined not by the mechanical concentration of cells from sea water during the new ice formation, but by photosynthesis and growth of the ice algae themselves.

It was shown (Melnikov, 1995) that the existence of oscillations is significant for the phenomena under study, because it implies the existence of a double-way flow of liquid phases from the ice into the water and from the water into the ice. The significance is enhanced by the fact that the drainage channels, occurring at a density of 50-200 m^{-2} (Lake and Lewis, 1970; Wakatsuchi and Ono, 1983), occupy a considerable part of the ice volume. As shown by in-situ observations (Saito and Ono, 1980), the brine channels are most intensively developed at a high rate of ice formation; there will thus be more channels in the rapidly growing young ice than in the slowly growing lower layers of the thick 1-year ice. In both cases, however, the oscillations cover most of the sea ice interior.

The drainage effect is relevant not only to dissolved substances, but also to suspended materials such as phytoplankton cells. During the period under study, a large amount of living and dead organic materials are probably flown out from the sea ice thickness into the underlying sea water as a result of brine drainage. This phenomenon is likely to play an important ecological role by providing food sources in winter conditions to the invertebrates associated with the underlying sea ice surface (Menshenina and Melnikov, 1995). Food composition was shown to be very similar for copepods living at this time of the year under the sea ice surface, such as *Metridia gerlachei, Rhincalanus gigas, Calanus propinquus,* and *Calanoides acutus* (Pasternak, 1995). The list of diatoms identified in their guts corresponds to the dominant species found within the sea ice in the present study. Continued SCUBA diving over the period of observations also revealed the main distribution features of animals associated with the bottom ice surface. It was shown that under-ice current and bottom sea ice topography are major factors influencing the behaviour and distribution of the young stages of animals such as krill, *Euphausia superba* (Melnikov and Spiridonov, 1996), fish larvae and juvelines, e.g., *Cryodraco atkinsoni, Pagothenia brachisoma, Neopagetopsis ionah* (Evseenko, 1994), to which ice provides a biological substrate for feeding, escaping from predators etc. These results also indicate that sea ice algae developing during the austral winter in the Antarctic sea ice zone should be considered an important factor in future biological models of the Southern Ocean.

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