Ice Flora (Bottom Type): A Mechanism of Primary Production in Polar Seas and the Growth of Diatoms in Sea Ice[1]

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ABSTRACT. A field survey off Barrow in the summer of 1964 revealed that sea ice in the Artic develops a layered structure through the growth of diatoms. The diatoms increase in brine solutions which occur in the microfissures between fine crystals of sea ice and form a brown-coloured layer near the bottom.

The chlorophyll content of the layer studied was 120 μg/l., or one hundred times greater than that of the sea water under the ice, leading to the hypothesis that the most important production of the Arctic is in sea ice, especially in spring and in early summer. Studies were also made of the flora of diatoms and of the mechanism of sea-ice degradation as related to its biological effects. In this paper arctic and antarctic conditions are compared.

RÉSUMÉ. *Flore de la glace (type basal): mécanisme de production première dans les mers polaires et croissance des diatomées dans la glace de mer.* Durant l'été de 1964, une étude effectuée au large de Barrow a révélé que, dans l'Arctique, la glace de mer présente une structure stratifiée par la croissance de diatomées. Ces diatomées se multiplient dans les solutions salines des microfissures entre les fins cristaux de la glace et forment une couche brune près de la surface inférieure.

Le contenu chlorophyllien de la couche étudiée était de 120 μg par litre, c'est-à-dire cent fois plus grand que celui de l'eau de mer sous la glace, ce qui permet d'émettre l'hypothèse que, dans l'Arctique, la production première se fait dans la glace de mer. surtout au printemps et au début de l'été. Des études ont aussi été menées sur la flore des diatomées et le mécanisme de dégradation de la glace lié aux effets biologiques; on a finalement comparé les conditions arctiques et antarctiques.

РЕЗЮМЕ. *Флора льда донного типа: механизм первичной продукции в полярных морях и рост диатомовых в морском льду.* Обследование моря при селении Барроу летом 1964 г. показало, что, благодаря росту диатомовых, морской лед в Арктике приобретает слоистую структуру. Диатомовые растут в соляиых растворах, в микроскопических трещинках между микрокристаллами морского льда и образуют бурый пласт у дна.

Образование хлорофилла в исследуемом пласте было 120 микрограммов/литр, или сто раз больше, чем в морской воде подо льдом, факт, ведущий к гипотезе, что первичная продукция в Арктике начинается в морском льду, в особенности весной и в начале лета, Флора диатомовых тоже была исследована, и механизм деградации льда был объяснен биологическими процессами; арктические и антарктические условия были сравнены.

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INTRODUCTION

It has been reported by Meguro (1962) that groups of diatoms have been found growing in the sherbet-like layer between upper snow and one-year-old ice in the summer pack ice off Lutzow-Holm Bay; the same has been reported by Burkholder and Mandelli (1965) near Palmer Peninsula, Antarctica.

Another type of ice algal community which forms a brownish layer at the bottom of sea ice has been reported near Devon Island in the Arctic by Apollonio (1961), near McMurdo Sound in the Antarctic by Bunt (1963a,b), and by us in Lutzow-Holm Bay, Antarctica (unpublished report).

There may be some question as to the use of the term "plankton ice" for these ice micro algal communities, but we found it convenient to use it in our previous reports; in the present paper the term "bottom-type plankton ice" is used to show that it is one of the series of papers and also to differentiate the ice algal community at the bottom of sea ice from that at the surface.

This paper constitutes a study of arctic summer sea ice in the vicinity of Barrow, to determine the ecological conditions of plant growth in polar sea ice (which has often been considered a cold biological desert), to investigate the primary production in sea ice in the Arctic, and to compare arctic and antarctic "plankton ice."

METHOD OF SAMPLING

About 13 sea-ice cores were obtained with a SIPRE coring auger and the samples were divided into several portions. Thirty samples of coloured-ice fragments and several samples of surface-pool water and of sea water under the ice were also collected. The ice samples were melted and immediately filtered with filter paper; chloride, phosphate-P, and dissolved silicate content were determined at the Arctic Research Laboratory at Barrow. Chlorophyll-*a* content was determined in Japan. Some of the coloured-ice samples were sliced and directly photographed in the cold room. All the collected samples were fixed with formalin for taxonomic work and for counting of cell numbers. Field surveys and chemical studies were carried out by Meguro and Ito; diatoms were identified by Fukushima.

EXPERIMENTAL

Chloride content was determined by electrical conductivity using a Denkikagaku liquid ohm meter and standard sea water.

The phosphate content was determined by the standard molybdenum blue method, comparing standard KH_2PO_4 solutions according to Saijo (1962) and using the Klett-Summerson photoelectric colorimeter. The error was about 0.004 mg. P/l.

The dissolved silicate content was determined by the standard yellow silicomolybdate method, comparing standard Na_2SiF_6 solutions and using the same apparatus. This method was not sensitive enough for the determination of the silicate content in the middle part of the sea ice because of the low concentration of dissolved silicate. The error was about 0.1 mg. SiO_2/l.

The chlorophyll-*a* concentration was determined according to the method of Saijo (1962). Diatoms were collected on filter papers (Toyoroshi No. 5 A) by suction immediately after the sea ice was melted. The filter papers were exposed to hot steam for five minutes, then dried and stored for about two months in a dark desiccator until the analysis in Japan. The filter papers were extracted three times with 10 ml. each of 80 per cent aqueous acetone in the presence of one drop of concentrated hydrochloric acid.

The acetone solution was extracted with 30 ml. of benzene. The benzene solution was washed with water to remove any dissolved acetone, and dried over anhydrous sodium sulphate. The absorption intensity of the benzene solution was measured at 665 mμ by a spectrophotometer (Hitachi ETU 2-A) as pheophytin-*a*.

The cell numbers of diatoms and the numbers of microdust in ice-melt water samples which had been fixed with formalin were counted in Japan using a Fuchs Rosenthal chemocytometer.

ICE CONDITION OFF BARROW

The sea ice was first surveyed on foot from 2 to 15 July 1964, to a distance of several hundred metres from the shore around the Arctic Research Laboratory at Barrow. During that period, ablation of the snow cover on the ice was complete and the ice surface was soiled with dust from the land; selective melting of the dust-soiled part of the ice was proceeding, with the result that many round pools and mushroom-shaped projections were formed. At the end of July, open water gradually appeared along the beach line and the pack ice began drifting off to the North. From 16 July to 3 August the ice survey was carried out in pack ice from 5 to 10 miles off the coast between Point Lay (69°05′N., 157°36′W.) and Point Barrow (71°05′N., 157°36 W.) on board the icebreaker C.C.G.S. *Camsell*. The air temperature at noon during the cruise was between 0°C. and 8°C., and the district was almost covered with heavy pack ice. Pack ice is a mixture of various kinds of sea ice: hard polar ice (more than 5 m. thick); one-year ice; ice that is two or more years old; pressure ridges, and small fragments thereof. The heterogeneity of arctic sea ice is shown in Fig. 1. The surfaces

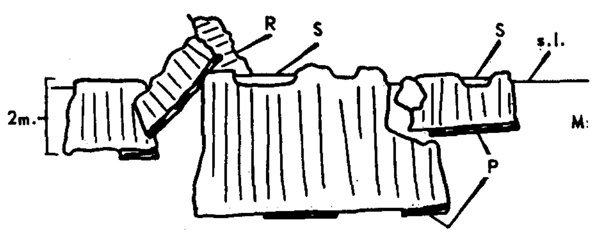

FIG. 1 Sketch of arctic sea ice in summer. S: surface pools; R: Pressure ridges; s.l.: sea level; M: middle layer of sea ice; P: plankton-coloured layer at the bottom.

of all types of ice were melted and the snow cover was ablated. There were many round pools of from 2 to 20 m. in diameter and several centimetres in depth; the depth of some extended to the sea water below. These pools showed that the ablation of the sea-ice surface had been considerable. Observations from a helicopter confirmed that the same ice conditions continued north as far as the flight range of the helicopter (about 20 miles).

The arctic summer *sea ice* near Barrow resembled the antarctic *fast ice* that had developed near the shore or adjacent to the shelf ice in Lutzow-Holm Bay. The similarity between the two lay in their bare ice surface and small pool formation in midsummer, and in the plankton-coloured layer near their bottom surface, although the antarctic fast ice was more homogeneous in thickness (Fukushima and Meguro, unpublished work). However, the arctic *sea ice* was different from the antarctic *pack ice* seen over a very wide area several miles off Lutzow-Holm Bay in that a thick snow layer covered the surface of the latter and few pools were seen even in midsummer; an added difference was that a plankton-coloured layer had formed between this snow layer and the pack ice (Meguro 1962).

These similarities and differences are thought to be due to the differences in snow precipitation during winter and spring. The precipitation is low in both the Arctic and the fast-ice areas of Antarctica, whereas there is greater precipitation in the pack-ice areas of the Antarctic.

PLANKTON-COLOURED LAYER AT THE BOTTOM OF SEA ICE

The profiles of sea ice were first examined when ice was broken and turned upside down by the icebreaker. This examination revealed that the arctic sea ice off Barrow had a yellowish-brown layer at the bottom. A preliminary microscopic observation of this coloured layer showed that it contained many diatoms and that the yellowish-brown colour was due to the pigments of the algae. Soiled ice often presented a similar brownish colour which, however, was observed mainly at the surface and in the centre and could be easily distinguished from the plankton-coloured layer by means of microscopic observation.

Diatom enrichment was found up to 30 cm. from the bottom of the ice, but no further. The brownish colour gradually became more intense towards the bottom surface, but maximum colour intensity was found several centimetres above it. The diatoms were found in colonies and the size of the colonies became smaller and the ice became harder according to the decrease in colour intensity.

In some of the ice, many small holes (0.2 mm. to 1 cm. in diameter) were visible to the naked eye near the bottom surface, and large diatom colonies of several millimetres at the inner cell walls of the holes were seen as brown spots (see Fig. 2). Very often a thin, colourless, smooth ice layer covered the bottom surface and thus these diatom colonies were not always in direct contact with the sea water under the ice. At the end of July, the coloured layer became soft and separated easily from the upper ice; because of its

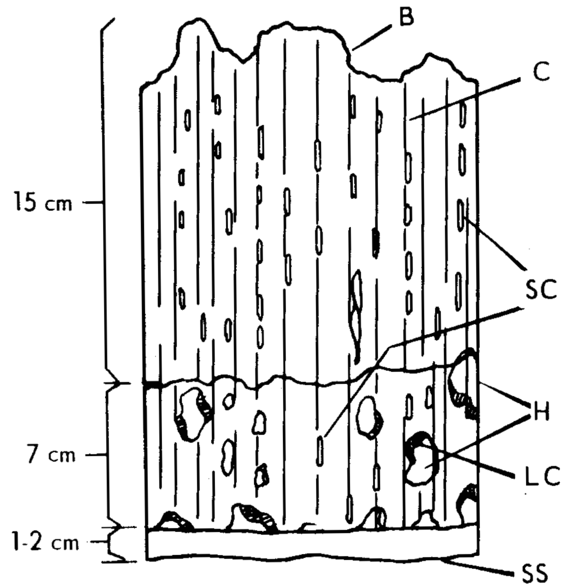

FIG. 2 Example of fragments of plankton-coloured layer at the bottom of the sea ice. B: broken, rough and ridged; C: vertical lined ice crystals; SC: small diatom colonies; H: holes of 0.2 mm. to 1 cm. dia.; LC: large colonies; SS: smooth bottom surface.

fragility, sampling by SIPRE corer was difficult or pratically impossible. However, we could get a core sample of the upper ice, which, when it had been split by the icebreaker, had first confirmed the existence of the

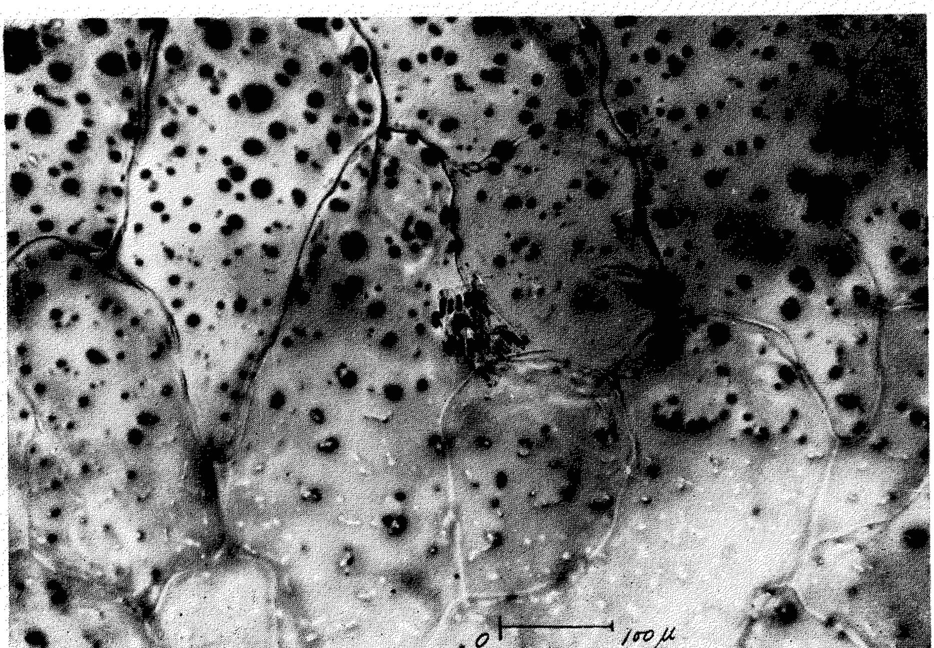

FIG. 3 A diatom colony at an early stage of development between ice crystals. Diatoms are arranged side by side while the single cell is subdividing. Photograph shows the ice sliced horizontally and across the crystals that extend vertically. The rods at the centre are diatoms; black round areas scattered in ice crystals are air bubbles; net-like lines are crystal boundaries.

coloured bottom layer; also, many fragments of coloured ice could be collected directly from sea ice that had been overturned, or from the open water between drifting ice floes.

The relation of floating fragments to the original sea ice was determined from the shape of those fragments; micro ice crystals ran vertically, and most of the fragments had one smooth side, which suggested long contact with sea water at the bottom surface of the original sea ice, as well as a rough, ridged side, which showed recent detachment from the original ice.

The coloured ice was sliced in the cold room without melting and the microstructure of the ice habitat and the sate of the diatoms in it were studied by microscope (see photomicrographs, Figs 3, 4, and 5). As in the case of upper sea ice, the coloured layer was composed of a number of vertically oriented ice crystals, and many micro and mega fissures existed between them; within the fissures were brine solutions and air pockets. The brine solution was found to be a microhabitat within which the diatoms divided and formed colonies. The existence of the colonies, which had probably divided from a single cell, showed that these diatoms were not mere prisoners in the ice and that they were, in fact, growing. Also, grazing by zooplankton was found to be highly restricted, because the structure of the ice habitat apparently did not allow them to enter.

The average chlorophyll-*a* content of the coloured layer was 120 μg/l. and the maximum was 427 μg/l., as is shown in Table 1. This value was

FIG. 4 The number of diatoms has increased in a larger fissure between ice crystals; the simple flora are probably from a single cell. Here the ice has been sliced vertically.

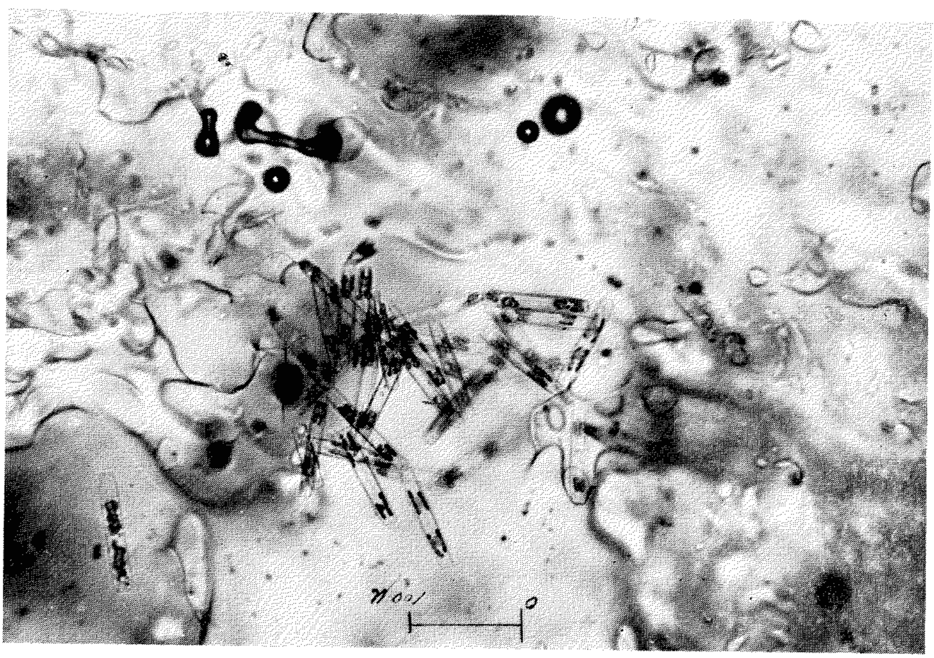

FIG. 5 Advanced stage of melting; the fissure is enlarged. Photograph clearly shows the distribution of chloroplasts and other microstructure in the cells of the diatoms.

TABLE 1. Chlorophyll-*a* and nutrient salt concentration of plankton coloured layer at the bottom of sea ice off Wainwright, Alaska (70°55′N., 159°12′E.).

Sampling Date	*Chlorophyll-a* $\mu g/l.$	*Chloride* *o/oo*	*Phosphate-P* *P mg./l.*	*Silicate-Si* SiO_2 *mg./l.*
27 July 1964	180.0	2.8	0.075	1.5
	221.0	1.6	0.07	2.1
	91.5	0.62	0.025	0.5
	93.6	1.4	0.07	0.8
	251.0	2.6	0.01	2.1
	427.0	—	—	—
	41.0	1.1	0.01	0.7
	36.4	0.25	0.01	0.4
29 July 1964	33.0	0.59	0.01	0.6
	72.0	0.59	0.02	1.0
	62.7	0.64	0.01	0.8
	118.0	0.12	0.02	0.8
	47.0	1.8	0.01	0.4
	10.2	0.55	0.01	0.4
Average	120.3	1.13	0.027	0.93

from 40 to more than 100 times greater than that of sea water around the ice, as is shown in Table 2. The high chlorophyll-*a* concentration suggests

TABLE 2. Average content of chlorophyll-*a* and nutrient elements in various sections of sea ice and sea water collected off Barrow in July and August 1964.

	Chlorophyll-a $\mu g/l.$	*Chloride* $^{0}/_{00}$	*Phosphorous P* $\mu g/l.$ *Phosphate-P*	**Diatom-P*	*Silicon Si mg./l.* *Dissolved silicate-Si*	**Diatom-Si*
Pool water at the surface of sea ice.	0.3	0.79	2.0	0.5	0.12	0.006–0.009:
Middle section of sea ice.	trace	0.92	9.3	—	0.07	—
Plankton-coloured layer at the bottom of sea ice.	120.3	1.13	27.0	204.0	0.44	2.4–3.7
Sea water around sea ice just after melting.	3.1	4.71	10.0	5.3	0.05	0.06–0.09
Sea water in open lead.	2.1	13.3	17.0	3.6	0.14	0.04–0.06

*Diatom-P and Diatom-Si are the elements of diatoms. The values are calculated from chlorophyll-*a* content of the samples according to Parsons *et al.* (1961). P/ch-a=1.7 and Si/ch-a=9.4 in *Coscinodiscus* sp.; P/ch-a=1.7 and Si/ch-a=14.3 in *Skeltnema Costatum*.

that the ice habitat does not merely permit survival, but is actually conducive to growth.

In the structure of its water-in-ice system, the coloured layer of the arctic *sea ice* resembled that of antarctic *fast ice* in Lutzow-Holm Bay (Fukushima and Meguro, unpublished work) and at McMurdo Sound (Bunt 1963b); arctic *sea ice* differed from antarctic *pack ice* in that in the case of the latter, the sea water absorbed the snow layer, formed a coloured layer, and possessed the structure of an ice-in-water system.

FLORA OF MICROALGAE GROWING IN THE COLOURED LAYER AT THE BOTTOM OF ARCTIC SEA ICE

The phytoplankton growing in the coloured layer of the sea ice around Barrow were composed of a group of diatoms among which no other algae were seen. Eleven species of *Navicula*, 7 species of *Pinnularia*, 2 species of *Pleurosigma*, and 1 species each of *Amphiprora*, *Gomphonema*, *Nitzschia*, and *Stenoneis* were identified, as is shown in Table 3.

In our antarctic study (Fukushima and Meguro 1966), 13 species of diatoms were identified in a similar type of coloured layer at the bottom of sea ice in Lutzow-Holm Bay. Among them, *Amphipleura rutilans v. Antarctica*, *A. kufferathii*, *Nitzschia Stellata*, and *Pleurosigma* sp. were dominant.

TABLE 3. Flora of the diatoms found in the plankton-coloured layer at the bottom of arctic sea ice off Barrow.

Amphiprora kryophila
Gomphonema exiguum v. arctica
Navicula algida
N. crucigeroides
N. directa
N. gracilis v. inaequalis
N. kjellmanii
N. obtusa
N. transitans
N. transitans v. derasa
N. transitans v. erosa
N. trigoncephla
N. valida
Nitzschia lavuensis
Pinnularia quadratarea
P. quadratarea v. biconstracta
P. quadratarea v. capitata
P. quadratarea v. constricta
P. quadratarea v. stuxbergii
P. semiinflata
P. semiinflata v. decipiens
Pleurosigma stuxbergii
P. stuxbergii v. rhomboides
Stenoneis inconspiqua

In another type of coloured layer, located beneath the snow cover on the pack ice off Lutzow-Holm Bay, 12 species of diatoms were identified; among them, *Fragilariopsis cylindrica* and *F. curta* were dominant.

Our arctic samples from the Barrow district were limited in number, but with a wider range of sampling and with greater numbers of samples, other diatom species may be found in the future. We have observed an interesting resemblance between antarctic and arctic ice flora and this resemblance can be outlined as follows: (1) both consist of more than ten species of diatoms; (2) these species are not new species, but are commonly found in sea water around ice; and (3) they are mostly spindle- or rod-shaped diatoms (other types of diatoms are sometimes found, but they are very few in number). The diversity of species suggests that living conditions are not so severe as to require special adaptation on the part of these rod-shaped diatoms; and yet on the other hand, conditions are not so mild as to allow other kinds of algae or other species of diatoms to flourish.

THE TEMPERATURE AND OSMOTIC PRESSURE OF THE MICROHABITAT IN ICE

As was revealed in our microscopic observations, the habitat in sea ice is a microbrine cell encased in ice crystals. This means that the brine solution, air, and crystals of H_2O are in a state of thermodynamic equilibrium at a given temperature. Although direct determination might be impossible, this state of equilibrium enables us to calculate the salt concentration of the brine solution at a given temperature, when that temperature is below the freezing point, or to calculate the temperature of the brine solution, which is the same as the melting point of ice when solar radiation causes local melting of the ice at the brine.

In winter, the air temperature is below the freezing point of sea water and ice crystals grow both at the bottom of the sea ice and at the wall of the inner brine cell pocket. The additional ice crystal formation in the micro cells, which are full of brine, leads to an increase in the saline concentration, which reaches a new state of equilibrium at the decreased temperature.

From the biological viewpoint, winter is a dark season in the Arctic, and any photosynthesis by plants or any growth of vegetable cell is impossible. Ecological interest is therefore concentrated on the question as to whether a diatom seed, which may be trapped in the ice while it is forming, can survive the winter.

The temperatures at the top and at the bottom of sea ice are considered to be almost the same as those of the atmosphere and of sea water, respectively.

In January and December, the mean minimum air temperature is about -30°C., according to Reed (1958), and the temperature of the sea water is about −1.8°C., or at freezing point. If the temperature gradient of sea ice from the top to the bottom is linear, then the temperature of brine located at any given distance from the bottom surface can be roughly calculated according to the thickness of the sea ice and the air temperature. Once this temperature is determined, the salinity of brine, hence osmotic pressure, can be calculated from the function (I) of depression of freezing point of sea water according to Miyake (1939), and the relation between salinity of sea water and osmotic pressure, according to Harvey (1960):

$$T = -55S \tag{I}$$

Where S = salinity (grams of salt per gram of sea water), and

T = freezing point.

The results of this calculation are shown in Table 4. These results show that the temperature of a brine cell within 30 cm. of the bottom of the sea ice should not be below -5°C., which is quite mild; but they also show that the osmotic pressure change caused by a slight decrease in the temperature of the brine solution is from 20 to 70 atoms, which is quite drastic for cell membrane.

The nutrient salt concentration of the brine solution can also be calculated if we assume that the concentrations of phosphate and dissolved silicate in relation to the chloride content of the brine solution in sea ice is the same in winter and summer. The results, as given in Table 4, suggest

TABLE 4. Physical and chemical environment of brine cells near the bottom of sea ice in winter.

Distance from the bottom of sea ice.	*Temperature °C.*	*Salinity 0/00*	*Phosphate-P P mg./l.*	*Silicate-Si SiO_2 mg./l.*	*Osmotic Pressure. Atom*
5 cm.	−1.75	18.0	0.18	3.0	c.20
10 cm.	−2.61	26.2	0.26	4.0	—
30 cm.	−4.45	44.7	0.45	7.0	c.70

These values are not determined, but are calculated under the following assumptions: (1) thickness of the sea ice is 2m.; (2) air temperature is −20°C.; (3) water temperature, under the ice, is −1.7°C.; (4) heat conductivity of the ice is vertically constant; and (5) the relative concentrations of phosphate and dissolved silicate to salinity are the same as those in sea ice in August.

that the nutrient concentration in microbrine is high enough for trapped diatoms to start growing. It is interesting that the factor which limits the survival of trapped diatoms in winter seems to be neither extremely low temperature nor low concentration of nutrient salts, but drastic osmotic pressure change. This is probably one of the reasons why the coloured layer always occurs near the bottom surface of sea ice.

When the sun starts to shine, the arctic sea ice begins to melt on the surface, and its temperature, from top to bottom, becomes about −1.7°C. The temperature gradient disappears and the conduction of heat from the surface becomes negligible. Therefore, energy for the melting of the sea ice around the brine must be supplied solely by absorption of the sunlight penetrating the ice; thus, the coloured section of sea ice melts far more quickly than does the transparent part. As melting proceeds, the salinity of the brine decreases, thus keeping the temperature quite stable. This promotes the active increase of diatoms and the accumulation of chlorophyll, and therefore results in the acceleration of partial melting in the coloured layer near the bottom.

THE TRANSPORTATION AND ACCUMULATION OF NUTRIENT ELEMENTS IN THE PLANKTON-COLOURED LAYER

The melt water of coloured ice was a light yellowish-brown diatom suspension. The diatoms and microdust were collected on filter paper by the filtration procedure described above. The extremely high chlorophyll-*a* concentration of the acetone extracts showed high concentrations, in the coloured layer, of elements of which diatoms are composed, elements such as phosphorous and silicon. The quantity of the elements in the diatom body was roughly calculated from the chlorophyll-*a* content, using the Table of Parsons *et al.* (1961), and is shown in Table 2 under the headings *Diatom-P* and *Diatom-Si*.

The dissolved silicate and phosphate in the filtrate were determined and are also shown in Table 2, for purposes of comparison. These forms of phosphorous and silicon are considered nutriment which is available for diatoms contained in the coloured layer at the moment of sampling. However, they were not so highly concentrated as were the elements which composed the diatom body, although phosphate and dissolved silicate in the plankton-coloured layer were slightly higher in concentration than they were in other parts of the sea ice. For example, the diatom-P of coloured ice, by calculation, was about 204 μg P/l., which is about 7 times higher than the phosphate-P in the same layer, about 20 times higher than the phosphate-P in the centre part of the sea ice, and about 12 times higher than the phosphate-P in the sea water in open lead among the ice floes. With respect to the silicon distribution, the same tendency was observed: diatom-Si in the plankton-coloured layer was about 2.4–3.7 mg. Si/l., which was from 5 to 9 times higher than the dissolved silicate in the same layer, and about 35 to 52 times higher than that in the centre section of the sea ice.

The above results mean that for phytoplankton to complete blooming in the coloured layer, most of the nutriments must be supplied, though the initial concentration of the nutriment in brine is enough for the diatoms to start growing.

Three possibilities are considered for the mechanism of nutrient supply:

1) *The bacterial conversion of organic compounds such as colloids contained in sea ice apart from living diatoms.* The higher concentration of phosphate in the plankton-coloured layer of sea ice may be attributed to bacterial

activity, although the slow rate of mineralization at $-1.7°$C. cannot be considered high enough to explain the total nutrient supply.

2) *The penetration of nutriments from sea water under the ice.* In the coloured layer at the bottom of sea ice this may not be impossible. However, penetration seems to be far more limited in arctic sea ice than it is in the sherbet-like snow layer in the antarctic pack ice, because of the difficulty of diffusion through the capillaric pathways between ice crystals into the brine, whose chloride content is supposed to be fairly high. The observation that the most densely diatom-populated zone was often found not on the bottom surface, but in the brine located several centimetres from that surface, also suggests the existence of a main route of nutrient supply other than the direct penetration of sea water. Although this kind of nutrient supply may be limited for diatoms inside the ice, it does not deny the direct utilization of the nutriment of sea water by diatoms attached just at the bottom and sides of the ice.

3) *The nutrient supply accompanied by the desaltation of sea ice.* This is considered to be the most important source of supply and is discussed below.

CALCULATION OF THE AMOUNT OF NUTRIENT SALTS WHICH PENETRATES THE BOTTOM SURFACE WITH THE DESALTATION OF SEA ICE

Ringer (Sverdrup *et al.* 1942, p. 218) described the process of desaltation of sea ice as follows: "In rapidly frozen sea ice the cells containing the brine are large or numerous. If the temperature rises, the ice surrounding the cells melts and the separated salt crystals are dissolved. But before complete solution has taken place the brine cells may join, permitting the brine to trickle down through the ice. If, on the other hand, the temperature rises to 0°C. all the salt dissolves, the cells grow so large that the ice becomes porous, and all the brine trickles down. In this way old ice becomes fresh and can be used as a source of potable water."

According to Malmgren (1927), the distribution of chloride in sea ice collected in early spring showed the highest concentration at the surface of the ice and a gradual decrease to the bottom. The average chloride content was 2.4‰. This distribution of chloride in the ice was explained as follows: "The amount of brine in the ice is related to the rate of ice formation or the temperature of freezing before desaltation has taken place in spring."

On the other hand, in summer at Barrow it was found that sea ice, just before the state of degradation, showed low chloride content at the surface and a gradual increase to the bottom as the result of desaltation. In this season, the average chloride content was 0.9‰ and therefore less than half of that of the April sea ice reported by Malmgren (1927), as is shown in Fig. 6.

If the chloride in sea ice in April near Barrow is the same as that determined by Malmgren (1927), then the amount of brine that penetrates the

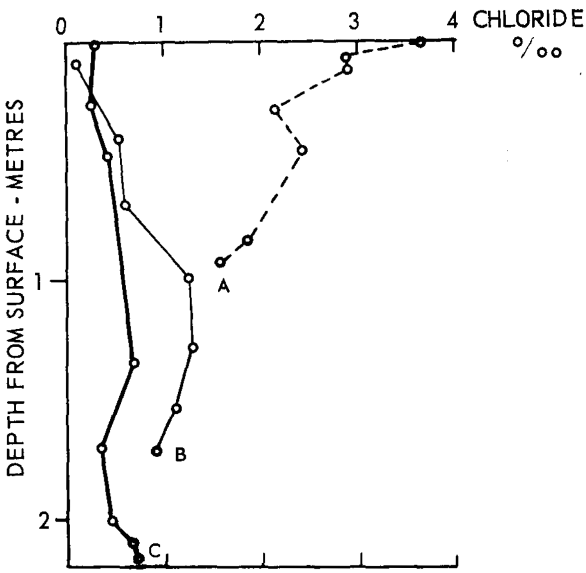

FIG. 6 Vertical distribution of chloride in arctic sea ice; seasonal change, April to July, showing descending brine. A: chloride content in April according to Malmgren (1927); B. collected at Barrow (70°20′N., 156°46′E.) 11 July 1964; C: collected off Wainwright (70°57′N., 158°58′E) 31 July 1964.

bottom surface can be calculated from the difference in average chloride content between spring sea ice and summer sea ice. If we further assume that the nutrient ratio of chloride in sea ice in April is the same as that of sea ice in August, the total amount of nutrient salt, N, in brine which is supplied from upper sea ice can be calculated by the following equations:

$$N = A \times \frac{b-a}{a} \times V \qquad \text{(II)}$$

where a is the chloride content of the middle section of sea ice in August,
b is the chloride content of the middle section of sea ice in April,
A is the concentration of nutrient salt in sea ice in August,
and V is the volume of the sea ice in August.

As shown in Table 2:

a was 0.92 °/oo,
and A: Phosphate-P was 0.0093 mg. P/l.,
Dissolved silicate-Si was 0.07 mg. Si/l.

According to Malmgren (1927):
b was 2.4 °/oo.

Therefore, according to equation (II):

$$N\ (\text{Phosphate}) = 0.0093 \times \frac{2.4 - 0.92}{0.92} \times V = 0.015\ Vmg.,$$

and $$N\ (\text{Silicate}) = 0.07 \times \frac{2.4 - 0.92}{0.92} \times V = 0.113\ Vmg.,$$

where $\mathcal{N}$ (Phosphate) and $\mathcal{N}$ (Silicate) are the total phosphate and silicate supplied from the upper ice.

If the diatoms in the coloured layer at the bottom live only on the nutriment supplied in the above-mentioned way, then $\mathcal{N}$ in equation (II) is the maximum nutriment available to them. Thus, the maximum thickness of the coloured layer, C max, can be calculated from the thickness of sea ice above that layer and the average phosphorous (or silicon) composing the diatom bodies and other inorganic phosphate contained in the coloured layer:

$$C_{\text{max}} = \frac{\mathcal{N}(\text{Silicate})}{Si(c)} \times d \times \frac{1}{\text{V}} = 8.9\text{–}6.1 \text{ cm.},$$

and

$$C_{\text{max}} = \frac{\mathcal{N}(\text{Phosphate})}{P(c)} \times d \times \frac{1}{\text{V}} = 14 \text{ cm.},$$

where d is the average thickness of sea ice in our field survey (about 2.3 m.); $P(c)$ is phosphate-P and diatom-P (totalling about 0.23 mg. P/l.) of the coloured layer in August; $Si(c)$ is silicate-Si and diatom-Si of the coloured layer in August (totalling about 2.8–4.1 mg. Si/l.). Another type of silicon compound, such as colloidal silicic acid, may also be utilized by diatoms.

Although there are still problems left in the calculation based on the silicate analysis, the maximum thickness of the coloured layer calculated from the phosphorous concentration agreed roughly with the results of our field survey, that is to say, the coloured layers that were seen at the bottom of sea ice about 2 to 4 m. thick ranged from 5 to 30 cm. in thickness.

Thus, the top layer of sea ice is considered a kind of nutrient reservoir which, with the desaltation of sea ice, supplies nutriments gradually. Carbonate, ammonium, and other sea-water soluble nutriments must be supplied in the same way.

LIGHT CONDITIONS

Many investigators have reported that the light intensity under sea ice is decreased considerably by reflection at the surface and by absorption of light by snow cover and sea ice. For example, Bunt (1963b) reported that in McMurdo Sound the light intensity under sea ice of 4 to 5 m. in thickness was only 0.2 to 8 foot candles in summer. We have not yet measured the light intensity at the plankton-coloured layer in the Arctic, but around Barrow the thickness of the sea ice was from 2 to 4 m., and the light intensity of the coloured layer is supposed to be not so far from that which is found under sea ice in McMurdo Sound. The variation in thickness of the sea ice and the existence of the same diatom species in the surface water of the area suggest that these diatom species are tolerant of or adaptable to weak light and various other light conditions.

However, it should be noted that weak light conditions at the plankton-coloured layer represent the highest light intensity available to the diatoms during ice cover; moreover, by growing in sea ice diatoms can use the available light energy more effectively than they can in the sea water under the ice.

Furthermore, once the coloured layer is formed, the intensity of light under the ice should be further reduced, especially in the wave length, through absorption by chlorophyll and other photosynthetic pigments.

The seasonal change in the light that is supplied to diatoms, the length of the days, the thickness of the sea ice, and the air temperature around Barrow are shown in Fig. 7, according to Reed (1958). It is dark from

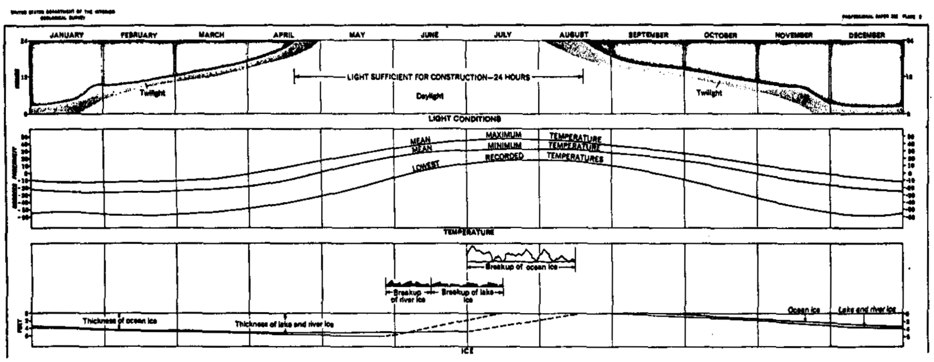

FIG. 7 Solar radiation, air temperature, and thickness of sea-, river- and lake-ice throughout the year, Barrow, Alaska. The minimum thickness of sea ice on open water is seen at the end of August which shows a time lag of two and a half months after the period of maximum solar radiation in the middle of July. Reprinted from: U.S. Department of The Interior, Geological Survey. Professional Paper 301. Plate 2. (Reed 1958).

November to January, then in April the days become longer and the solar radiation becomes stronger, reaching a maximum in June; in August the light decreases to the April level. The decrease in the thickness of ice shows a time lag of two and a half months after the increase of solar radiation, and open water is seen for less than two months, from the beginning of daylight August to the middle of September.

Considering solar radiation and the thickness of sea ice, diatoms in the Arctic can utilize daylight most efficiently if they grow in sea ice from April to July, and then live in sea water in August and September.

Apollonio (1961) reported a high chlorophyll concentration (89 μg /l.) at the bottom surface of sea ice at Devon Island in June. And although the plankton-coloured layer has not been observed before June, it is speculated that diatoms might start growing earlier because at the beginning of May, as well as end at the of July, solar radiation is probably strong enough.

PRIMARY PRODUCTION IN ICE

As in warmer seas, the study of primary production in the Arctic Ocean has been based upon the determination of phytoplankton in sea water. According to the observations of English (1963) on the drift station *Alfa*

(1956-58) in the high Arctic, phytoplankton appear in the water for only a short time in summer. From the end of September until the end of May chlorophyll-*a* concentrations were quite low (less than 0.2 μg/l.); they suddenly increased at the end of June, showing the maximum (2 μg/l.) simultaneously with the disappearance of snow cover at the ice surface. Bursa (1961) also reported the sudden appearance of phytoplankton in the summer at Igloolik in the Canadian Arctic. The conventional observations of phytoplankton in sea water have shown that generally primary production in the Arctic is extremely low, though sometimes the sudden appearance of local short-term blooming of phytoplankton around ice floes has been observed.

However, there is a contradiction between poor primary production and the abundance of zooplankton and sea animals in the region, as suggested by Johnson (1962).

In our ice observations, the chlorophyll-*a* content of sea ice was about 24 mg. per m.^{2}, by rough calculation from the average thickness (20 cm.) and the average chlorophyll-*a* concentration (120 μg/l.) of the plankton-coloured layer. The large crop of phytoplankton in the ice shows that the primary production of the Arctic Ocean is not necessarily the smallest when compared with that of other oceans.

In order to get further information on the relation between phytoplankton in sea water and phytoplankton in sea ice, two bottles of surface sea water were sampled and the chlorophyll-*a*, chloride, and nutrient salt concentrations were determined (see Table 2). One sample was collected in heavy pack from narrow open water, just after sea-ice degradation; it is of low chloride content (4.7°/₀₀, which is less than one third of that of usual sea water) due to dilution by ice-melt water. Another sample was collected from an open lead, of more than 30 m. in width, in pack ice, and its chloride content was 13.3 °/₀₀. This had also been diluted by ice-melt water, but was of higher chloride content due to the mixing of deeper sea water than before. These samples showed chorophyll-*a* concentrations of 3.1 and 2.1 μg/l., respectively. These were of almost the same order as the maximum chlorophyll-*a* concentration of sea water under the ice in the high Arctic reported by English (1963), and might be referred to as the "blooming of phytoplankton."

The high concentrations of chlorophyll-*a* in sea water diluted with ice-melt water suggest that the considerable proportion of phytoplankton in the pack-ice region may be the result of the liberation of diatoms grown in ice.

As discussed previously, diatoms in ice are considered free from grazing, so the standing crop in the ice is not "the resultant balance between the rate at which they have been produced and the rate at which they have been eaten," but is probably the net primary production in sea ice for the season. The degradation of the coloured part of sea ice means the liberation into the sea of all the integrated standing crop since spring. In spite of the relatively lower rate of primary production throughout the year, the blooming of phytoplankton might subsequently induce local blooming of zooplankton around summer pack ice, which might attract larger sea animals.

In conclusion, we propose the following hypothesis on the primary production of "bottom-type plankton ice" (ice flora, bottom type) as a mechanism of the Arctic Ocean as shown in Fig. 8. We submit that diatoms

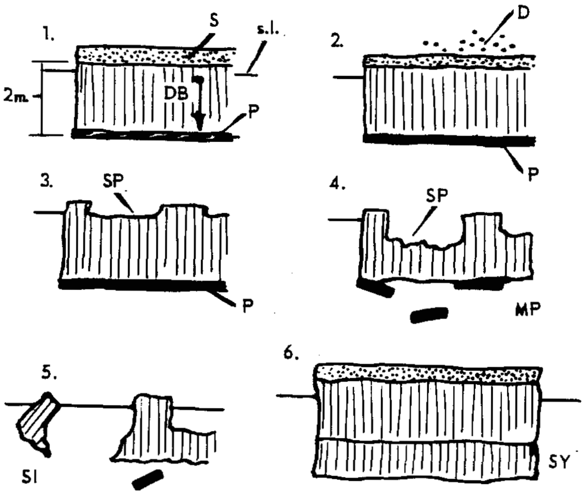

FIG. 8 A presented mechanism of ice flora (bottom type) in the Arctic; development of plankton-coloured layer at the bottom and dust-precipitated pools at the surface. S: snow; s.l.: sea level; DB: descending brine; P: plankton-coloured layer; D: dust from land; SP: development of surface pools; MP: melting-off of plankton-coloured layer; SI: degradation of sea ice; SY: formation of second-year ice.

frozen into sea ice during their formation probably survive the winter by means of cyst formation and start growing as soon as solar radiation is restored in the spring, gradually forming a plankton-coloured layer at the bottom of the sea ice. Accompanied by a gradual decrease both in snow cover and in the upper part of the sea ice as a result of increased solar radiation, the amount of light arriving at the plankton-coloured layer increases and rots the layer through selective absorption of solar energy by pigments. At last, the plankton-coloured layer gets detached or broken up by wave-buffeting and this results in a sudden blooming of phytoplankton in the water under the ice.

The biological environment of the coloured layer of sea ice may be summarized as follows:

1) Relatively stable temperature ($-3°$ to $0°$C.).

2) Enough nutrient salt concentration at the start of growth and nutrient supply during growth.

3) Variable osmotic pressure.

4) Weak light conditions, but stronger than light conditions in sea water under the ice.

5) Absence of or limited grazing by zooplankton.

6) Probable abundance of organic matter.

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