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PRIMARY PRODUCTION IN THE FROZEN LAKE BALATON

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The characteristics of the aquatic environment are deeply changed by the ice cover, isolating the water body from the athmosphere. It prevents the formation of waves, the exchange of gases and alters the light conditions. The changed light conditions exert an influence in the first place on the primary production.

In shallow lakes besides that of the planktonic algae the production of benthic algae is also of importance (HARGRAVE, 1969; HUNDING, 1971; HICKMAN, 1971). According to ENTZ (1954), FELFÖLDY (1963) and OLÁH (1972) considerable algal biomass and chlorophyll are to be found at the bottom of Lake Balaton. This mass is probably the highest in winter, when the mud surface is covered by a brownish algal carpet visible to the naked eye. On the basis of the investigations in the early fifties ENTZ (1954) estimated the mass of microphytobenthos in winter to be 10 g/m^2. On the production of algae under the ice cover only a single information is available, in January—March 1956 in six weeks 4.6 mg/litre O_2 increase was detected in the water under the ice-cover by ENTZ and LUKACSOVICS (1957).

This paper offers data, collected in the winter of 1972—1973 on the light conditions, chlorophyll content and primary production of phytoplankton and phytobenthos and on the oxigen content of water under ice.

Methods

The investigations were carried at 500 m eastwards from the Institute in the pelagic zone of the lake. Light was measured by Gemware submarine photometer. The vertical distribution of the μ-algae was determined by the method of DENOYELLES (1968). The chlorophyll was measured according to STRICKLAND and PARSONS (1968).

Production of the phytoplankton. To measure the primary production of the phytoplankton 100 ml samples were taken from 25, 100, 200, and 300 cm depths. After adding 20 μCi $Na_2{}^{14}CO_3$, they were in situ exposed from 10^h to 14^h. The bottles, lowered to different depths were tied to the end of a Z shaped iron rod. The lower, horizontal part of this rod reached as far as 150 cm under the intact ice cover. The small hole cut in the ice was covered by snow. This way the samples got into natural light conditions. Further handling of samples, radioactivity measurement and calculations were carried out as described earlier (HERODEK and TAMÁS, 1973).

Production of the phytobenthos. It was measured both by ^{14}C and O_2 techniques. Mud was brought to the surface by a HARGRAVE's (1969) sampler. The mud in its original structure was covered with water from the bottom.

By ^{14}C technique glass tubes fitted with 19 mm normal grounds on both ends were used. Their diameter was 17 mm, the length between the normal grounds 100 mm. The tubes were stuck into the mud in Hargrave's sampler to get a 2 cm thick core. The water filled the tubes to the rim. The tubes were stoppered from below, and some water was drawn off just to make room for the 1 ml water, with which the isotope was introduced. Into each tube 20 μCi Na_2CO_3 was injected in a way that the label should be mixed with water above the mud as evenly as possible. The tubes were now stoppered also from above, and the glass stoppers were fixed by thin elastic tapes. The tubes serving as dark parallels were covered with aluminium sheets. The tubes fitted on stand were lowered to the bottom through a small hole which was then masked by ice. The tubes were exposed from 11^h to 14^h. After exposal the water and the upper 3 mm mud layer were separated from the bulk of the mud, which would hinder the radioactivity measurement. The water containing the upper mud layer, the labeled hydrocarbonate and the algae was filled up with inactive Balaton-water to 50 ml, and vigorously shaken, then 5 ml aliquot of it was filtered through a membrane filter. After the samples 50 ml, previously filtered inactive Balaton-water was passed through the filters, then they were exposed to the fumes of concentrated HCl for 4 min, in order to remove the contaminating labeled hydrocarbonate. The filters were dissolved in BRAY solution, and the remaining thin mud-alga film was homogenized in POTTER—ELVEHJEM apparatus. Radioactivity was measured by liquid scintillation. Sedimentation was prevented by adding 4 percent Cab-O-Sil to the scintillation liquid. The carbon uptake was calculated from the total carbonic acid content of the water and the radioactivity of algae.

In experiments by O_2 technique glass cylinders of 50 mm diameter and 200 mm length were used. The cylinders were stuck 5 cm deep into mud, obtained by HARGRAVE's sampler. The tubes containing the intact sediment core and the water above it were stoppered bubble free by rubber corks. The upper cork was provided with spill-way. Dark controls were covered by aluminium sheets. The glass cylinders fitted on stands were in situ exposed. After exposal the water was drawn off from the cylinders avoiding contact with air. The oxygen concentration was determined by the original WINKLER method and by its Na-azide modification. The same result was obtained by both methods proving that by the applied procedure reduced materials had no disturbing effect.

Ice conditions

The lake was overfrozen on the 28^{th} December, 1973. The ice was glass-like transparent except on places of drift-ice accumulation. Snowing started on the 16^{th} January and the 25 cm thick ice was covered by a 4 cm thick snow-blanket. One week later the snow thawed and on the 31^{st} January the 18 cm thick ice opaque from small holes and cracks was covered by cca.

1 cm water. Three days later the water disappeared, the ice became opaque. On the 6th February only the upper 2 cm of the ice was of continuous structure, the lower layer was in the state of desintegration. On the 8th February the ice-cover went to pieces, and on the 12th February large areas were already ice-free.

Results

Light (Table I). On the 28th December light was measured under the thin ice lamellae formed in the freezing water. The high extinction was due to the sediment, swirled up by the strong wind of the previous day. Light conditions were similar to those generally found in Lake Balaton at windy weather (Felföldy and Kalkó, 1958; Entz and Fillinger, 1961; Herodek and Tamás 1973). Less than 1 percent of surface light penetrated to 1 m depth. On the 17th January the 25 cm thick ice was covered by 4 cm fresh snow and 9 percent of the light got through the snow and ice. Entz and Filliger (1962) found 7 percent of the surface light intensity under the ice covered by 8—10 cm thick fresh snow. This way, in spite of the clear water, the illumination of the deeper layers was very low. The snow-free ice transmitted the half of the light and as in the rather clear water under the ice the light intensity decreased only to its one fifth, about 1/10 of the surface illumination was measured at the bottom. In the period April—September only in two cases of the 13 measurements was found as much light at the bottom as here, while in 10 cases the illumination at the bottom was less than 1 percent (Herodek and Tamás, 1973). In Lake Balaton the light conditions under the snow-covered ice are worse, under snow-free ice much better than in the open lake.

TABLE I

Illumination in the ice-covered lake (lux)

Depth, cm	28. Dec. 1972	17. Jan. 1973	18. Jan. 1973	31. Jan. 1973	5. Febr. 1973	6. Febr. 1973
0	30 600	13 500	10 500	5 500	20 500	34 500
25	21 350	1 250	1 640	2 360	11 490	21 500
100	4 190	440	800	1 650	7 320	11 380
200	940	210	650	1 140	4 620	8 050
300	260	140	450	700	2 820	5 060
360 (bottom)	140	100	350	470	2 250	4 030

Chlorophyll content of the phytoplankton and the vertical distribution of μ-algae (Fig. 1). The chlorophyll content of the water, sampled under the ice cover was much lower than in samples originating from the open lake (Felföldy, 1963). In samples from 25 cm depth the chlorophyll was scarcely measurable. The chlorophyll content increased with depth. Perhaps this distribution of algae is responsible for the lack of production in the water layer nearest to the ice. The low chlorophyll content under the ice indicates a poorly developed phytoplankton. At the same time the 2—6 μ large μ-algae which are otherwise not present in considerable quantities in Lake Balaton

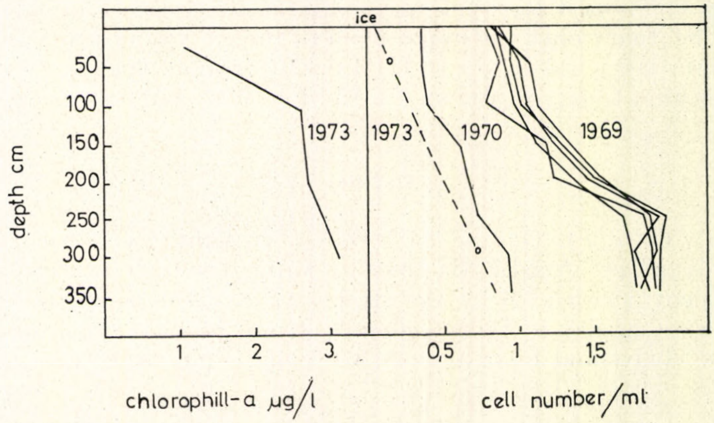

Fig. 1. Chlorophyll-a content of phytoplankton and vertical distribution of μ-algae

(OLÁH, 1970) were numerous. The surface of these tiny organisms is relatively large. They were found in the winter plankton of other lakes in great numbers (LUND, 1961; PENNAK, 1968; RODHE, 1955). Their presence indicates shortage of nutrients. The nutrients in low concentrations are better utilized by these organisms, than by larger algae. While in the unfrozen water the phytoplankton was in the average evenly distributed (HERODEK and TAMÁS, 1973) the number of μ-algae showed consequently an increase downwards during the investigations in different years.

Chlorophyll content of the phytobenthos. Only summer data were published on the chlorophyll content of the mud until now (OLÁH, 1972). In June 1972 the chlorophyll content of the 2 cm thick mud cores was 5—7 μg chlorophyll-a/g wet mud. In February 1972 the chlorophyll content was determined in mud samples from one point in front of the Institute and from three points in the Keszthely Bay *(Table II)*. Similar high values were found at all points.

TABLE II

The chlorophyll content of the microphytobenthos in February 1972
μg chlorophyll/g wet mud

	4. Febr. 1972 In front of the Institute	8. Febr. 1972 Keszthely Bay		
		point 1.	point 2.	point 3.
chlorophyll-a	46.9	40.0	43.8	38.1
chlorophyll-b	1.9	2.1	1.2	1.7
chlorophyll-c	40.9	38.5	32.4	39.6

The cores were 5 mm thick, therefore the μg/g values divided by two offer the results approximately in μg chlorophyll/cm^2. In 1973 the chlorophyll content of the mud was analyzed at two different times *(Table III)*, parallel with the measurement of the primary production of the benthos. In this case 5 mm thick cores with given surface (12 cm^2) were analyzed. This way the data

TABLE III

The chlorophyll content of the microphytobenthos in front of the Institute in the winter of 1973
μg/cm²

	31. January		5. February	
	point 1.	point 2.	point 1.	point 2.
chlorophyll-a	8.54	6.58	15.50	15.13
chlorophyll-b	0.10	0.09	0.96	1.13
chlorophyll-c	2.64	2.22	2.38	2.55

are directly comparable with those of the primary production also related to the surface area. The chlorophyll level was high, but lower than in the previous winter. On the 5th February the chlorophyll content was higher than on the 31st January, on the other hand the parallels of the same days showed similar values. In the samples there was much chlorophyll-c, characteristic for the diatoms.

Primary production of the phytoplankton (Fig. 2) The production of phytoplankton showed different pictures at the days investigated. On the 28th December the tin ice absorbed practically no light, and in strong sunshine at 25 cm depth photo-inhibition was found. The maximum was at 1 m depth, at 2 m the production was already somewhat lower, and at 3 m it was very low owing to the insufficient illumination in the turbid water. On the 17th January in the darkness under the snow-cover the maximum was in the highest level at 25 cm, but decreased downwards. This was the lowest production per surface area found in this lake. On the 31st January, under snow-free ice, the sequence of the production of the water layers was the opposite. The highest production was observed at 3 m, it decreased at 2 m and at 1 m, and at 25 cm under the ice there was practically no production. Under the snow-free ice the production per unit of surface area was 20 mg $C/m^2/h$. It is lower, than in the warm period (Herodek and Tamás, 1973) but not lower than usually in autumn.

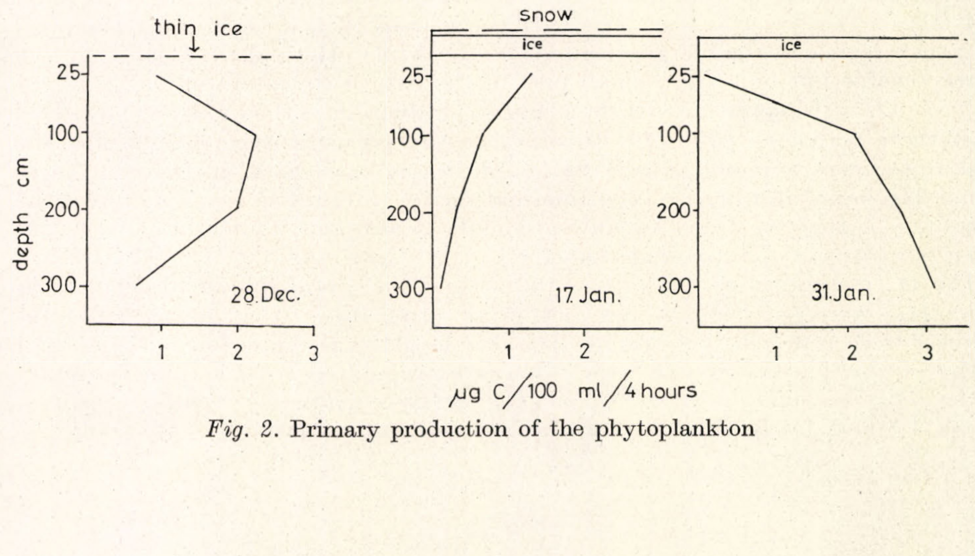

Fig. 2. Primary production of the phytoplankton

Primary production of the phytobenthos. We tried to measure the primary production of the benthos on the 26th April, and the 18th July by ^{14}C technique, and on the 13th July, 18th August and 20th September by O_2 method. No significant difference from the dark parallels was observed. Accordingly on these days there was no primary production in the benthos, or it was negligible as compared to that of the plankton. Production (463 mg O_2/m^2) was detected for the first time on the 13th October *(Fig. 3).* Oxygen consumption of the mud per the gross oxygen production, i.e. the R/P quotient was 0.52. In the case of mud the respiration of algae amounts to the smaller part of the total oxigen consumption, the bacteria and animals are responsible for the remainder. On the 14th December the oxigen production was consider-

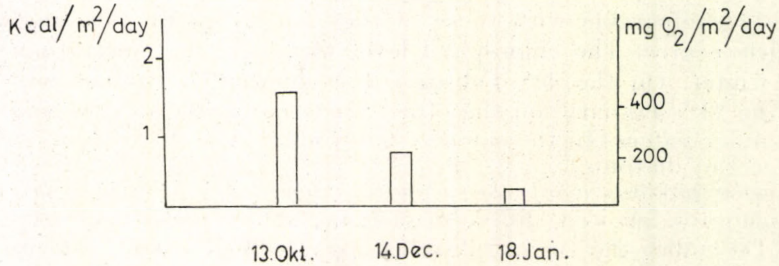

Fig. 3. Primary production of microphytobenthos in the unfrozen and the frozen, snow-covered lake. (Exposal for 24 hours)

ably lower, and already surpassed by the respiration (R/P = 1.62). After these measurements in open water the first 24 hours experiment under the ice cover was carried out on the 18th January. This day the ice was covered by 4 cm snow, and the light intensity on the bottom was 352 lux. On the previous day under similar conditions at 2 and 3 m depths there was practically no production in the phytoplankton. The gross production of the benthos, i.e. the value of the light cylinder minus the value of the dark cylinder was 66 mg O_2/m^2/day. The net production, i.e. the difference between the O_2 in the light cylinder at the beginning and at the end of the experiment was −257 mg O_2/m^2/day. It shows that by this low illumination the mud even if covered by the algal carpet decreases the oxygen content of the water. Here again algae could be responsible but only for a small part of the oxigen consumption.

After the snow thawed the primary production of the mud was measured at three occasions *(Fig. 4).* Contrary to the previous experiments now the samples were exposed not for 24 hours, but in case of ^{14}C method for three midday hours and in case of O_2 method for five midday hours. To express the results of the two types of measurements in common units they were converted to calories supposing that 1 g C = 10 Kcal and 1 g O_2 = 3.51 Kcal. The O_2 method gave the gross production. The values obtained by the ^{14}C method were between the net and gross productions they were. 5 percent lower than the gross production. The day length was taken for 10 hours, and the production during the exposals was extrapolated to this time to obtain the daily production. The ^{14}C and O_2 methods gave rather similar results, 3.6, 4.3 and 4.0 Kcal/m²/day on the three different days.

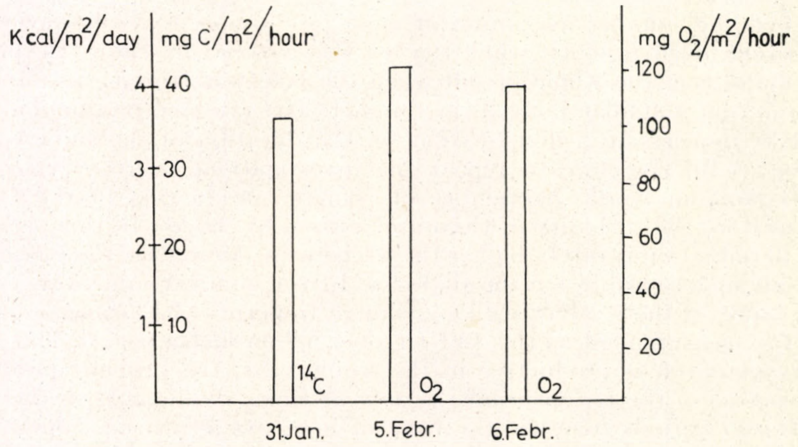

Fig. 4. Primary production of microphytobenthos in the lake covered by snow-free ice. (Exposal for the midday hours)

Oxygen content of the water. (Table IV). In the unfrozen lake the water was saturated by oxygen and became highly oversaturated when covered by ice indicating intensive photosynthesis in the frozen lake. On the 5th February the oxygen content was not higher than on the 18th January. This can be explained by the snow, covering the ice for a time in this period. In the darkness under the snow rather a decrease than an increase of oxygen content is expected.

TABLE IV

The O_2 concentration in the water of Lake Balaton

Date	Notice	Temperature	mg O_2/l
14. Dec.	no ice	5 °C	12.55
19. Dec.	no ice	4 °C	13.00
18. Jan.	ice cover	3 °C	22.59
5. Febr.	ice cover	3 °C	22.53

Discussion

The chlorophyll-a content of the phytoplankton related to surface area was 10 mg/m². This is with one order of magnitude lower than that of the benthos, where in February 1973 66—155 mg/m² was found. The primary production of the plankton and benthos, on the other hand, were similar; in case of plankton 20 mg C/m²/hour, in case of benthos 36 mg C/m²/hour. The total of the planktonic and benthic productions was 560 mg C/m²/day. In April—September the mean production of the phytoplankton was 413 mgC/m²/day, the maximal production was 588 mg C/m²/day (HERODEK and TAMÁS, 1973). As in this warm period no primary production was found in the benthos, the total of the productions of the planktonic and benthic algae was higher in the lake covered by snow-free ice than the average in the warm months, and approached the summer maximum of algal production. Since however there was a period, even if short, when the ice was covered by snow, the primary production during the whole period when the lake was frozen was about the same as during a similar interval in summer. The primary production of the frozen lake depends to a great extent on the duration of the snow cover, it would be useful therefore to repeat the investigations in other years, too.

The lack in April—September of primary production in the benthos is explained by the turbidity of the water caused by waves. In this period the bottom illumination is rarely higher than 1 percent. Moreover, the disturbance is by itself unfavourable for the diatoms. In the summer and even more in autumn however there are calms long enough to permit the formation of algal carpet. The measurement on the 13th October fell on such a period. Thus, while the phytoplankton is productive in the whole year, the primary production of the benthos in the unfrozen lake is only at times significant. In the frozen and unfrozen periods together the time of intensive benthic production can be estimated to roughly three months. At this time the extent of benthic primary production is similar to that of the plankton, the yearly production of microphytobenthos is therefore about one fourth of that of the phytoplankton.

The increase of oxygen concentration under the ice can serve as a measure of the production in the lake. If the 9.59 mg O_2/l increase between the measurements on the 19th December and 18th January took place after freezing of the lake on the 28th December then it corresponds to 1958 mg O_2/m^2/day or to 561 mg C/m^2/day net production. The total of the primary productions of the plankton and benthos as measured by ^{14}C technique on the 31st January was 560 mg C/m^2/day. In fact the agreement is not as tight as this since not the same "production" was measured by the two methods. The primary production measured by ^{14}C method is lower than the gross production only by the part of the newly incorporated carbon, burned by algae during the three hours of the experiment, i.e. about by 5 percent. The oxygen increase under the ice, on the other hand, was lower than the actual gross production by the oxygen consumption of all biotic and abiotic processes during the whole day.

In 3.5 m deep water the 9.59 mg O_2/l production corresponds to 33.6 g O_2/m^2 or to 11.8 g C/m^2. This carbon must exist somewhere in the form of organic material. As compared to this amount the biomass of the plankton is insignificant. Most likely the bulk of this carbon is present in the benthic algae. Dividing the 11.8 g/m^2 carbon by the 0.15 g/m^2 chlorophyll-a content of the benthic algae 78.7 is obtained. In different algae this quotient used to vary between 25 and 100. The 11.8 g C/m^2 net production corresponds to about 118 g biomass /m^2 which if extrapolated to the 600 km^2 surface of the lake provides 70 800 metric tons. The whole summer biomass of the lake was estimated by Entz (1954) to 30 000 metric tons. Accordingly the net increase of biomass in January 1973 was twice as high as the whole biomass in the summer of 1954. The mass of the phytoplankton and macrophytobenthos increased in the last two decades, still the biomass of the huge algal carpet, covering the bottom of the lake under favourable light conditions in winter is much larger than the sum of the masses of all planktonic algae and of the reed grasses taken all together. Owing to the algal carpet the biomass of the lake shows its maximum in winter, and this maximal value may serve as a useful index of eutophication.

Summary

Of the light one tenth was transmitted by ice covered by 4 cm snow and the half by snow-free ice. The water was rather clear under the ice, therefore in case of snow-free ice one tenth of the surface light reached the bottom. This illumination is higher than that in the unfrozen lake, where due to the turbidity caused by waves the bottom illumination is usually less than 1 percent.

The chlorophyll-a content of the water increased downwards. Related to surface it was 1 $\mu g/cm^2$. Similar vertical distribution was observed in the μ-algae, occuring in the water under the ice. The chlorophyll-a content of the bottom was 6.6—8.5 $\mu g/cm^2$ on the 31[st] January and 15.1—15.5 $\mu g/cm^2$ on the 5[th] February 1973.

When the ice was covered by snow the primary production of phytoplankton, measured by ^{14}C method, was 4 mg C/m^2/hour and decreased downwards. Under the snow-free ice it was 20 mg C/m^2/hour and increased downwards.

The production of the microphytobenthos was measured by both ^{14}C and O_2 methods. No production was found in April—September due to the turbidity of water. In the frozen lake when ice was covered by snow even the gross primary production in the benthos was very low. In case of snow-free ice intensive benthic photosynthesis was found. The primary production at three different days was 36 mg C/m^2/hour, 122 mg O_2/m^2/hour and 115 mg O_2/m^2/hour.

In the lake covered by snow-free ice the total primary production of the plankton and benthos was amounted to 560 mg C/m^2/day, which is similar to the summer maximum of planktonic production.

In the ice-covered lake the oxygen content of the water was with 9.6 mg/litre higher than before freezing, indicating the accumulation of high amounts of organic material.

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ELSŐDLEGES TERMELÉS A BALATON JEGE ALATT

Herodek Sándor és Oláh János

Összefoglalás

A 4 cm hóval borított 25 cm vastag jégtakaró a felületére eső fény egytizedét, a hómentes jég a felét engedte át. A jég alatti víz nagyon tiszta, ezért a hómentes jég alatt az aljzat megvilágítása a jég feletti megvilágítás egytizede. Hómentes jég alatt tehát jobb az aljzat megvilágítása, mint jég nélkül, amikor a hullámok okozta zavarosság miatt az esetek többségében kevesebb mint 1% fény jut az aljzatra.

A vízoszlop klorofill tartalma 1 μg klorofill-a/cm² volt, és felülről lefelé nőtt. Hasonló vertikális eloszlást mutattak a jég alatti vízben megfigyelhető μ algák is.

Az aljzaton 1973 I. 31-én 6,6—8,5, I. 5-én 15,1—15,5 μg klorofill-a/cm²-t találtunk.

Havas jég alatt a fitoplankton termelése 4 mg C/m²/óra volt, és felülről lefelé csökkent, hómentes jég alatt 20 mg C/m²/óra termelést mértünk, amely felülről lefelé növekedett. A fitoplankton termelését ^{14}C módszerrel mértük.

A fitobentosz termelését ^{14}C és O_2 módszerrel is mértük. Havas jég alatt a bentosz algái nem termeltek. Hómentes különböző napokon az iszap elsődleges termelése 36 mg C/m²/óra, 122 mg és 115 mg O_2/m²/óra volt.

Hómentes jég alatt a fitoplankton és fitobentosz együttes termelése 560 mg C/m²/nap volt, ami hasonló a fitoplankton termelésének nyári maximumához. Nyáron a bentoszban nem tudtunk elsődleges termelést kimutatni.

A jég alatt a víz oxigén tartalma 9,6 mg/liter-rel magasabb volt, mint befagyás előtt, ami nagy tömegű szerves anyag keletkezésére utal.