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FISHERY BOARD OF SWEDEN

INSTITUTE OF FRESHWATER RESEARCH

DROTTNINGHOLM

Report No 45

LUND 1964
CARL BLOMS BOKTRYCKERI A.-B.

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Contents

Limnological Studies in Hyttödammen

1. Physical and chemical conditions

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Contents

I. Introduction

In earlier articles information has been presented concerning Hyttödammen's zooplankton (Arnemo 1960), fish production in the years 1938—60 (Steffner 1961), higher aquatic vegetation (Arnemo and Norlin 1962) and bottom fauna (Norlin 1964). Various information is also given by Puke (1955, 1956, 1957 a and b). The aim of this article is to provide a survey of the physical and chemical environmental conditions in the pond. When collecting material for the present investigation samples for determination of the primary production, standing crop of zooplankton and food and growth of the fish were also collected. The results are intended for publication in subsequent parts of this series. When all the parts are completed, it may be possible to put forward points of view additional to those dealt with in this article, especially as regards the minor constituents.

II. Hyttödammen

The situation of Hyttödammen is shown in Fig. 1. The external conditions for the pond have been described by Arnemo and Norlin (1962, translated): "Hyttödammen is a pond (Swedish: naturdamm) which, since 1938, has

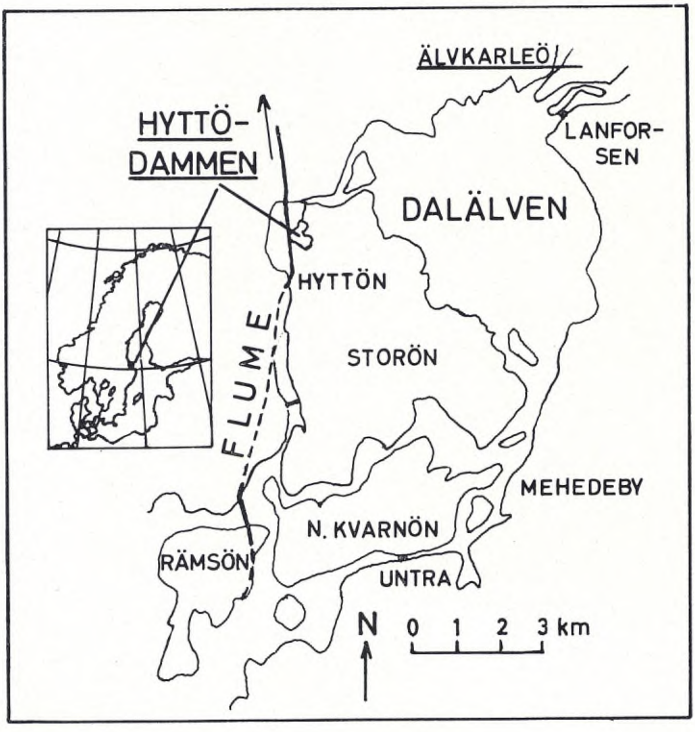


Fig. 1. Situation map. The flume consists partly of wood (———) and partly of a channel excavated in the soil (- - - - -).

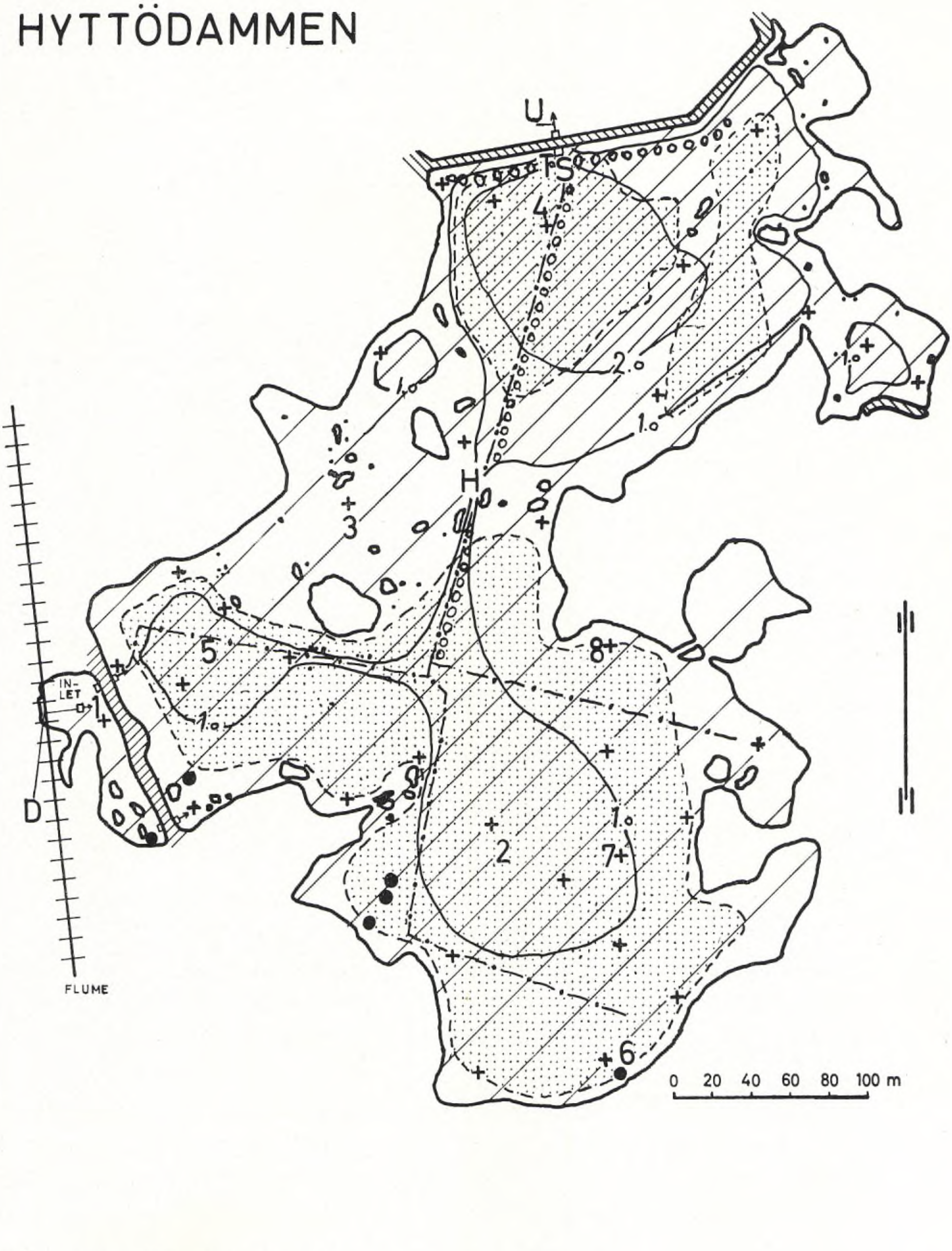


Fig. 2. HYTTÖDAMMEN. Key to the symbols:

T = thermograph. S = site for transparency measurements. ++++++++++++ = flume. ● = spring.
D, U, 1-8 = sites for chemical sampling. O O O O O = aeration tube. —·—·— = main ditch.
+ = site for special studies of $\varkappa$, pH, HCO_3.
▨ = 0-1 m, ▨ = 1-2 m, ▨ = > 2 m } depth. ⁘ = boundary of agriculture. ▨ = dam.

been used by the Hatchery at Älvkarleby (belonging to the Royal Fishery Board) for the rearing of one-summer-old salmon. The pond lies 13 km WSW of Älvkarleby Church and 20 km S of the town of Gävle. The pond obtains water partly from springs which open into it but mainly from the river Dalälv through a flume which runs past the pond and from which 80—100 l/sec is drawn off. The average depth of the pond is about 1 m with a maximum depth of 2.2 m at the outflow. . . . Before the pond came into being, the now dammed up area was covered partly by trees and boulders and partly by cultivated arable land. . . . The uppermost sediment in the entire pond consists of mould with rotting plant remains and silt. Beneath this layer, in the large bay lying to the south, is concealed a sand layer which has been dated by SANDEGREN and LUNDEGÅRDH (1949) to the late-glacial and post-glacial periods. Other parts of the pond and its nearest surroundings have, according to the same authors, moranic grit beneath the mull layer." Additional information is given in Fig. 2. In what follows the southeast bay is referred to as SE bay.

During the years of the investigation the pond has maintained a uniform size with an area of 12 ha and a volume of *c.* 135,000 m^3. In winter the volume of water is reduced by ice formation, as follows:

Thickness of ice (cm)	Volume of remaining water as $^0/_0$ of 135,000 m^3
10	90
20	80
30	71
40	62
50	53
60	45
70	38

The values are based on information from the adjustments which were made in connection with the construction of Hyttödammen. They served then for an estimation of the water volume at different heights of the dam.

Information on the filling and draining of the pond is given in Table 1, p. 9. It is clear from the table that the pond was also filled during the winters of 1960/61, 1961/62 and 1962/63. This is a departure from the usual procedure of the previous 22 years when the pond was drained during the winter, and also represents a departure from the account of the conditions given in earlier publications.

In winter 1960/61 salmon were overwintered as an experiment, since there was no place for them in the hatchery. Otherwise it would have been necessary to put them out in the Dalälv with very little chance of their reaching the smolt stage. The pond was filled so that the depth of the water at site 4 (see Fig. 2) was only about 1 m. The overwintering resulted in a survival of 17 $^0/_0$ of the salmon counted at the time of introduction in autumn 1960.

Table 1. Dates of filling, draining, removal of fish, air bubbling and sampling of water for chemical analysis.

	Commencement of filling with spring and melt water	Approx. depth of water at site 4 when Dalälv water was added.	Commencement of addition of Dalälv water	Date when pond full	Commencement of drainage	Date when drainage concluded with removal of fish	Period of aeration	Number of occasions of sampling for water chemical analysis, between filling and draining			
								Main series	Spring water	In C^{14} expts.	Special dets.
1959	Apr. 21	0.5 m	Apr. 30	May 26	Sept. 16	Oct. 7—12		1	2[1]		
1960	Apr. 21	0.8 m	May 13	June 1	Sept. 20	Oct. 17—20		10			
1960—61	Oct. 28	0.0 m	Oct. 28	Nov. 7[2]	Apr. 8	Apr. 14		3	5[1]		
1961—62	Apr. 17	0.2 m	Apr. 20	May 18	Apr. 16	May 7—9	Nov. 9—Apr. 26	15		2	8
1962—63	May 12	0.1 m	May 15	June 8	Apr. 17	May 2—4	Nov. 11—Apr. 19	5		6	5

[1] Samples taken after draining.
[2] The pond filled so that the depth at site 4 was only about 1 m.

The following information about fish production and overwintering is provided by Mr. N. G. STEFFNER (pers. com.).

In winter 1961/62 the conditions were quite different. During the summer a contagious disease had infected the hatchery. To combat this the entire hatchery was drained for several weeks for purification after release of the smolts in April. This meant that the fish had to be retained in Hyttödammen. Hence no removal of fish took place during autumn 1961 and until April 1962. On the basis of experience gained from the experimental overwintering the previous year, it was estimated that the chances of successful overwintering would be increased if the oxygen conditions were improved. In late autumn, diversion of Dalälv water into the flume is stopped to prevent freezing, thus cutting off the main source of water flow into Hyttödammen. As a result of the reduced supply of water coming only from the relatively oxygen-deficient springs, the oxygen conditions might reach a lethal level if nothing were done.

To improve the oxygen conditions, the pond was aerated from a plastic tube on the pond floor, as shown in Fig. 2. (See also the aerial photograph from Nov. 27, 1962 in Fig. 7.) Air was supplied from a compressor and bubbled out into the water from small holes evenly distributed along the plastic tube. The air bubbling prevented complete ice formation during even the most severe cold periods and thus also probably promoted aeration by surface exchange. The air bubbling caused continued circulation of the water column, which slowly cooled during the winter. Fifty-five per cent of the salmon and 42 % of the sea trout, based on the number of newly hatched fish exposed, survived the winter. The sea trout were few in number in relation to the salmon. The same was the case the following overwintering.

Since this overwintering was largely successful and, at the same time, some of the sea trout reached the smolt stage after only one year, fish were also overwintered in the pond in winter 1962/63. The results of this were 57 % survival of the sea trout and 18 % survival of the salmon. It is as yet too early to draw definite conclusions from the overwintering results because of possible after-effects in the form of changes in the summer conditions affecting the pond's production.

III. Meteorological conditions

Information on the air temperature (Gävle), precipitation (Gävle) and sunshine hours (Uppsala) is summarized in Figs. 3 and 5. The values were obtained from SMHI (Swedish Meteorological and Hydrological Institute) yearbooks 1959—62. The air temperatures show that the summer of 1961 was warmer than in 1962.

Precipitation, expressed as a percentage of the normal, shows that the

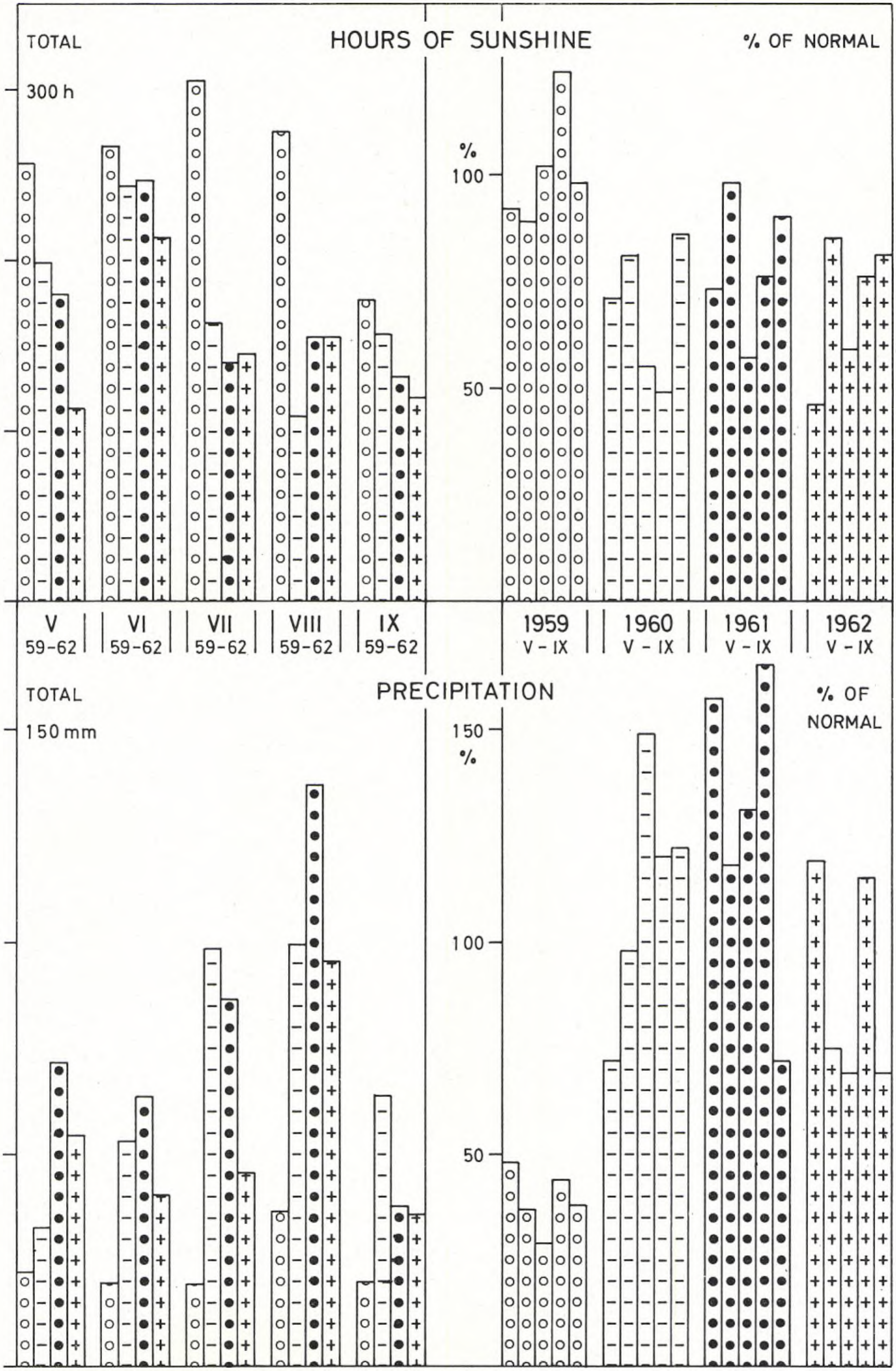


Fig. 3. Hours of sunshine at Uppsala. Precipitation at Gävle.

summer of 1959 was dry, 1960 and 1961 wet and 1962 about normal. The figures for precipitation in mm for the months May to September show that August was the wettest summer month for the years 1959—62. The two wet years, 1960 and 1961, have the highest values for each month, namely in May and June 1961, in July 1960, in August 1961 and in September 1960.

Sunshine hours were about normal. The highest values, expressed as a percentage of the normal, occurred in 1959. Of the other three years, 1961 had the next largest number of sunshine hours and 1960 and 1962 the smallest — and largely similar — numbers. Between May to September, 1959 had the highest values for each month. Very large differences in the conditions in 1960—62 occurred during July and August.

IV. Material and Methods

1. Field methods

All the sampling sites are shown together in Fig. 2. The times of collection of material during the years 1959—62 in the different periods when the pond was filled are given in Table 1.

To give a picture of the general features of the water chemistry in Hyttödammen, samples were taken at 7 main sites. These sites are the same as those described by ARNEMO (1960). The sites represent the following: Dalälv water in the flume (D), a small pond between the flume and the pond itself (1), the SE bay with a bottom of old ploughland (2), the area with a bottom of old boulder and forest land (3), the deepest area near the outlet (4); the surface=a, 1 m=b, the bottom 2.2 m=c and the outflow stream (U). In addition, samples have been taken at site H when only the area closest to the outlet was under water. H lies in the main ditch. In 1959 samples for water analysis were collected only once. From spring 1960 samples have been collected more or less regularly.

To enable a more detailed study to be made of the conditions in the area with dense vegetation and with different qualities of the supplied water (see p. 41) samples were taken in 1962 at approximately monthly intervals, from the following sites: 5 (affected by water from the Dalälv) and 6, 7 and 8 (affected by spring water and at different distances from the most important springs). Data from these sites are compared with the conditions at site 4, where vegetation is more or less absent.

Samples of the spring water for analysis were collected during the periods when the pond was dried out. Twenty-six such samples were collected.

After collection all the water samples for chemical analysis were stored in $^1/_2$- or 1-litre plastic bottles.

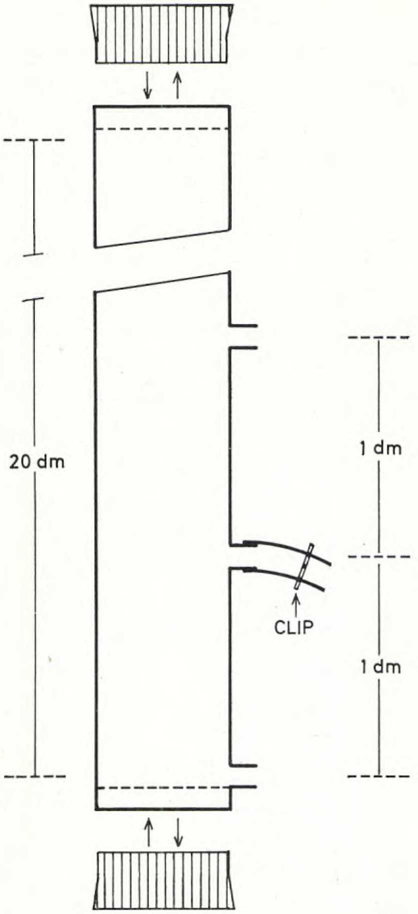


Fig. 4. Construction of the plexiglass sampling tube (Bērziņš).

At the beginning of the investigation, the water samples were collected with a Ruttner sampler, capacity 1.6 litres. After Dec. 4, 1961, the Ruttner sampler was used only for studying the vertical distribution at the deepest site (4). At the other sites samples were taken using a plexiglass tube, 2 m long and 62 mm in diameter. With such a tube samples of the complete water profile from surface to bottom can be collected in shallow sites. Such samples are more representative than samples taken with a Ruttner sampler. The subsample for analysis was taken after transference to a bucket or the like and mixing of the composite sample.

A similar tube was used for taking zooplankton samples in the littoral zone of Lake Erken by Mrs. E. ALMQUIST (pers. comm.).

To study the vertical distribution in shallow localities where a Ruttner sampler is not suitable, Dr. B. BĒRZIŅŠ (pers. comm.) used in his Aneboda investigations a plexiglass tube from which subsamples can be drawn off at different depths. He has been kind enough to put this apparatus at my disposal (see Fig. 4). Samples have been taken from depths of 0.1, 0.5 and 1.0 m. The number of samples is given in Table 1. A defect of this sampling method is that the diameter of the tube is too small for a single sample to fill a 1-litre bottle. For this four samples are necessary. Great care was taken in the field work to eliminate possible errors caused by this repeated sampling. Another disadvantage of this sampling method is that some mixing may occur as a result of air trapped in the subsampling tubes. This can be prevented by lowering the plexiglass tube obliquely so that the outlets of the subsampling tubes point downwards. If great care is taken, disturbances from the above sources can be avoided. The plexiglass tube seems to be more suitable than a Ruttner sampler for taking samples in shallow water where the stratification approaches a microstratification.

With the aid of the plexiglass tube composite samples can be taken from the surface to the bottom. This has been made use of in special studies of the horizontal heterogeneity of the specific conductivity of the water. The preliminary results of this investigation were described by ARNEMO and NORLIN (1962). A subsample was taken and the specific conductivity of this was measured with a bridge either in the laboratory (model: Leeds and Northrup 4866-S) or in the field (model: Normameter 185 RW) at 20° C in both cases. On each sampling occasion samples were taken at about 30 different sites distributed over the whole pond (see Fig. 2 where the most frequently used sites are marked). The investigation has been repeated at even intervals and the total number of sampling occasions is given in Table 1 beneath special dets. (determinations).

pH was measured in the field in 1961 in connection with special studies of horizontal heterogeneity of the water masses with a battery-powered Radiometer type PHM 24, and in the laboratory with a Radiometer type PHM 23 c.

A thermograph recorded temperature between May 25 1961—Jan. 10 1962 and June 6—Oct. 6 1962. During the former period, temperature was recorded at a depth of 1.5 m, and during the latter at 1.0 m. The sensitive body is a mercury-filled container for recording at a distance. The instrument was borrowed from SMHI. The accuracy was given as ±0.5° C. This was checked once a week, when the paper was changed, with a thermometer in a Ruttner sampler. The temperature at sampling was also measured with a thermometer in a Ruttner sampler.

Transparency was determined in the summers of 1961 and 1962 with a white Secchi-disc, 25 cm in diameter, and water telescope.

2. Laboratory methods

On the occasions on which the analyses were to be most comprehensive, the laboratory analyses comprised the determination of specific conductivity and pH (see above p. 44), alkalinity and the contents of sulphate, chloride, calcium, magnesium, sodium, potassium, phosphate- and total phosphorus, ammonium-, nitrite-, nitrate- and total nitrogen, total iron, silicon, and colour.

The laboratory methods follow the directions given by KARLGREN (1959; latest edition 1962). The following explanatory notes are provided for the different analyses.

In the samples in which the calcium content might have been too low for complete precipitation to occur, a known amount of calcium was added prior to precipitation. This applies particularly to the Dalälv water.

From the beginning up until sampling on June 13, 1962, total nitrogen was analysed according to LOHAMMAR (1938 pp. 31). At this method gave lower values than Kjeldahl digestion (see AHLGREN 1963 p. 2), the method of analysis was changed to the latter method. The content was determined photometrically after the addition of NESSLER's reagent.

Ammonium-nitrogen was determined photometrically, using pyrazolone.

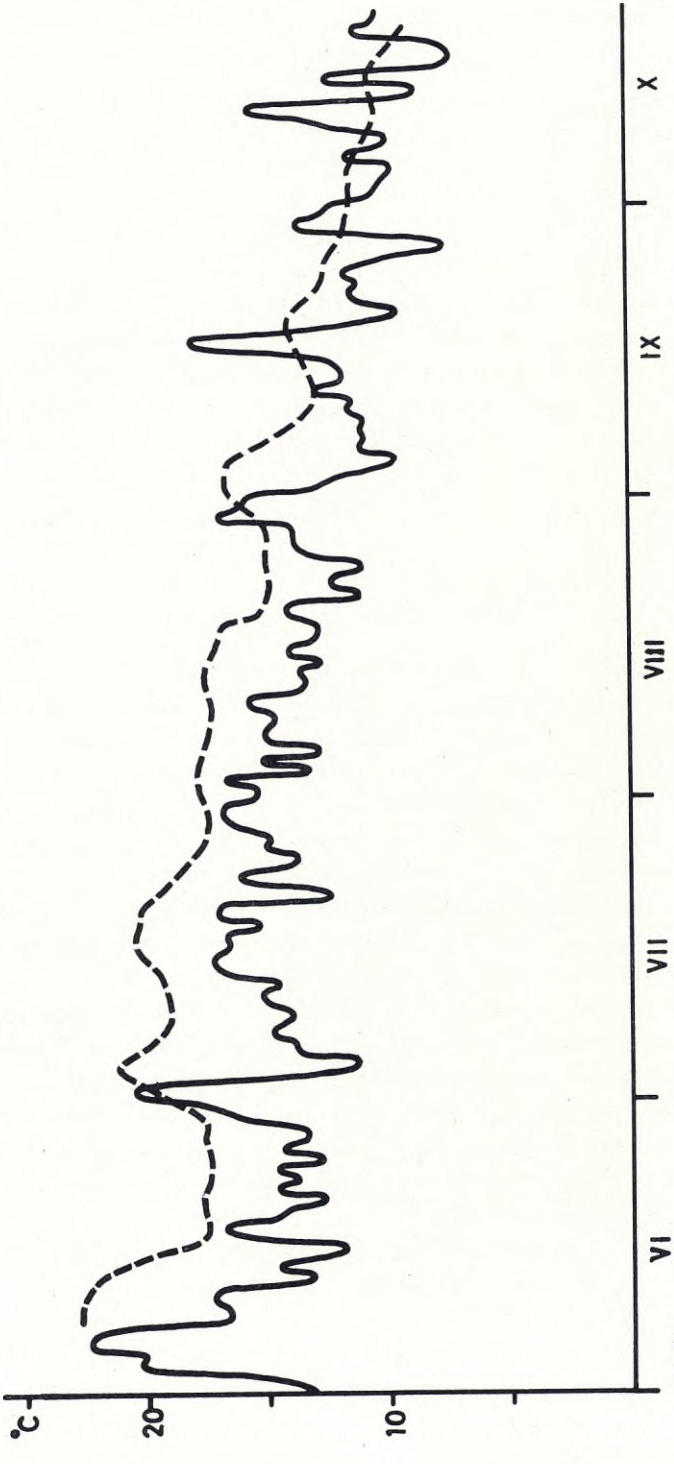
3. Construction of diagrams

The investigations of water chemistry consisted of studies of temporal variations at the sites D, 1, 2, 3, 4, U and in part H, and temporal and vertical variations at the sites 4, 5, 6, 7 and 8. In the latter investigation the samples were taken using the plexiglass tube (see Fig. 4). For each substance analysed there is, as a rule, a diagram for each of the two investigations: the first-mentioned investigation is as a rule shown on the left-hand page, while the latter is on the right. For references to the sites see page 12.

In the first-mentioned diagram, the development of the vegetation and ice is marked: for the vegetation the observations refer to the absolute dominant, *Sagittaria sagittifolia* L. The date given for the beginning of the vegetation is when the first leaves appear at the surface of the water, and the end of the period is taken as being when the stalks fall to the bottom. Despite the different conditions which occurred during the investigation, the time of development of the vegetation did not vary. The beginning of the ice is given as the time when the pond was first completely covered by ice. Draining and removal of the fish occurred before the break up of the ice. The maximum thickness of the ice was 70 cm.

The letters V, S and F give the times at which the pond was filled (V), drained (S) and the fish removed (F). D_1 indicates the time at which water ceased to run in the flume.

The sites have been distributed along the vertical axis in the order in which a body of water from the Dalälv, entering via the flume, would travel at a time when the vegetation is so well developed as to prevent mixing of the water in the horizontal direction. The distribution of the vegetation in Hyttö-


°C
20
10
1961
VI
VII
VIII
IX
X

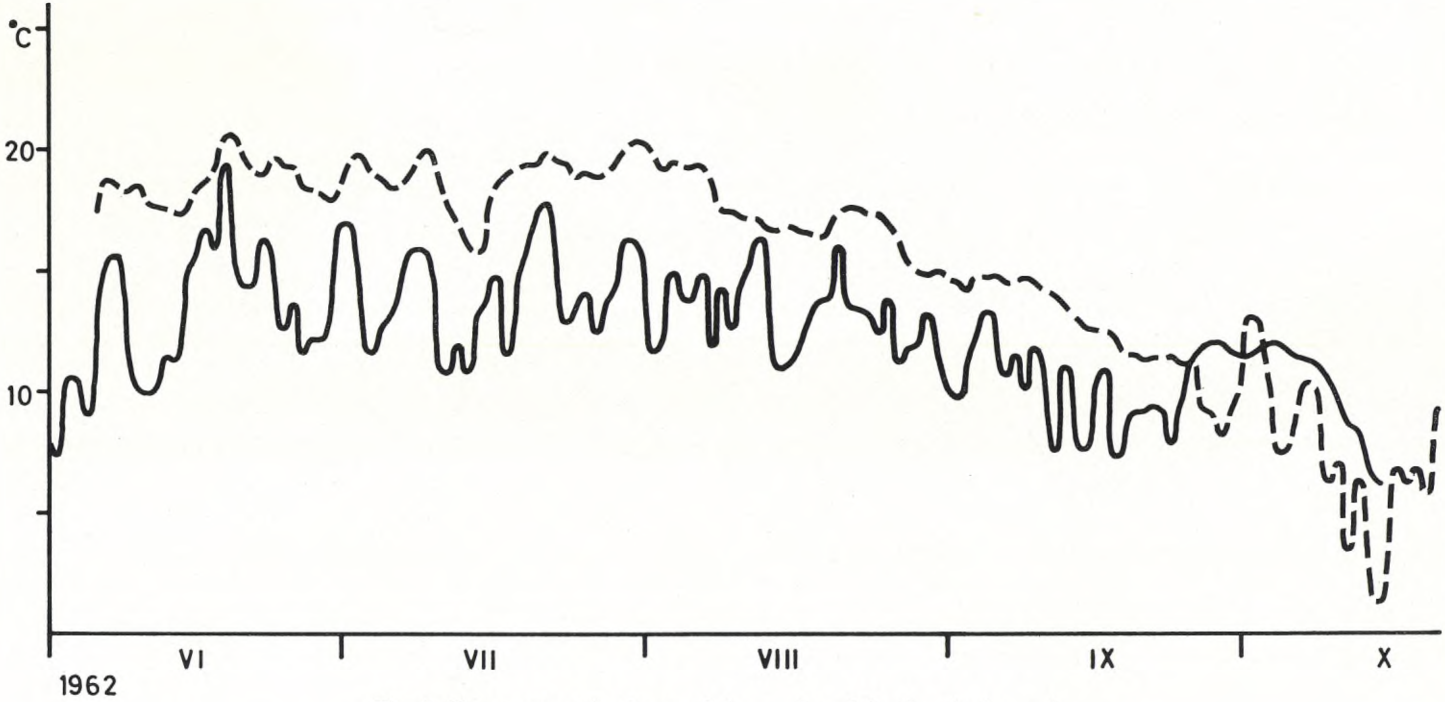


Fig. 5. Temperature in the pond (———) and in the air (- - - -).

dammen is given by ARNEMO and NORLIN (1962) and is also shown in the aerial photographs of Fig. 7. In the area around site 4, where the vegetation is sparse, mixing occurs freely, and water from the SE bay is also mixed-in there. Under the above-mentioned conditions this bay is hardly affected by Dalälv water and it obtains its character from the springs which open into it (see Fig. 2). When there is no vegetation the situation described above does not apply. Water from the Dalälv and the springs then mixes in more or less the whole of the pond's water mass. The distance between the sites in the diagram have therefore been chosen arbitrarily and are not in absolute units.

Site 2, which represents the conditions in the SE bay, has been separated from the sequence of the other sites by horizontal lines and has been introduced into this sequence at the point where the water from the SE bay has an effect.

Site 4 is represented by an average value of data from the surface and bottom water. No chemical stratification has been observed except for oxygen. Therefore, Fig. 11 differs from all the others. The vertical stratification at site 4 is also shown.

Isopletes, limiting different intervals of values have naturally had to be drawn diagrammatically. This is partly because of the distance between the sites, which as already stated is not given in absolute or relative units, and partly because with the drainage and filling there are insufficient analyses to provide a detailed picture of what happens at these times. However, this is of subordinate importance for this investigation, and the values lying nearest in time have been used for these periods. Nor is it possible to give the exact times of drying out or when the water reaches the different sites, but this is also of minor importance.

Various boundary lines have been drawn in the Figures. For specific conductivity the isopletes have been drawn so that the following intervals have been distinguished, with Dalälv water as starting point: $30—40 \cdot 10^{-6}$ (corresponding to the main range of variation of the Dalälv water), $40—50 \cdot 10^{-6}$, $50—100 \cdot 10^{-6}$, and $> 100 \cdot 10^{-6}$ (corresponding to an increasing degree of influence from water other than that of the Dalälv together with the effect of freezing).

For the major constituents no isopletes have been drawn for absolute values. This would not be appropriate, since the composition of water from the springs is different from that of Dalälv water (see p. 41). In addition, the vegetation has an effect because of accumulation of ions in different amounts in different tissues (see pp. 85). Therefore, instead, lines have been drawn which mark whether the ions in question occur in higher or lower concentrations than those given by standard composition (see RODHE 1949, p. 381) for the corresponding value of specific conductivity.

For the minor constituents arbitrary isopletes have been drawn, partly for different absolute contents, partly for ratio values.

V. Primary data

1. Temperature

The variation with time of the water temperature in the pond is shown in Fig. 5 as the daily averages from the continuous records. The average values for each 24 hour period have been calculated from 12 observations (one every two hours) taken from the charts. The curve for 1961 has been taken from NORLIN (1964). The mean daily air temperature at SMHI's station at Gävle, ca. 20 km N of Hyttödammen, for the corresponding period is given in the same Figure. The Figure demonstrates that the pond, because of its very small volume in relation to surface area, responds relatively quickly to changes in the air temperature. ARNEMO (1960) has also shown this by comparing the temperature of the incoming Dalälv water with that at some of the sampling sites in the pond. The Dalälv water responds more like a lake and is characterized by a delay in warming up in the spring and in cooling in the autumn. This is also shown by the values from different parts of the pond. These were obtained in connection with sampling with the Ruttner sampler 1960—62 and are shown in Table 2.

Table 2. Temperature at different sites 1960—62.

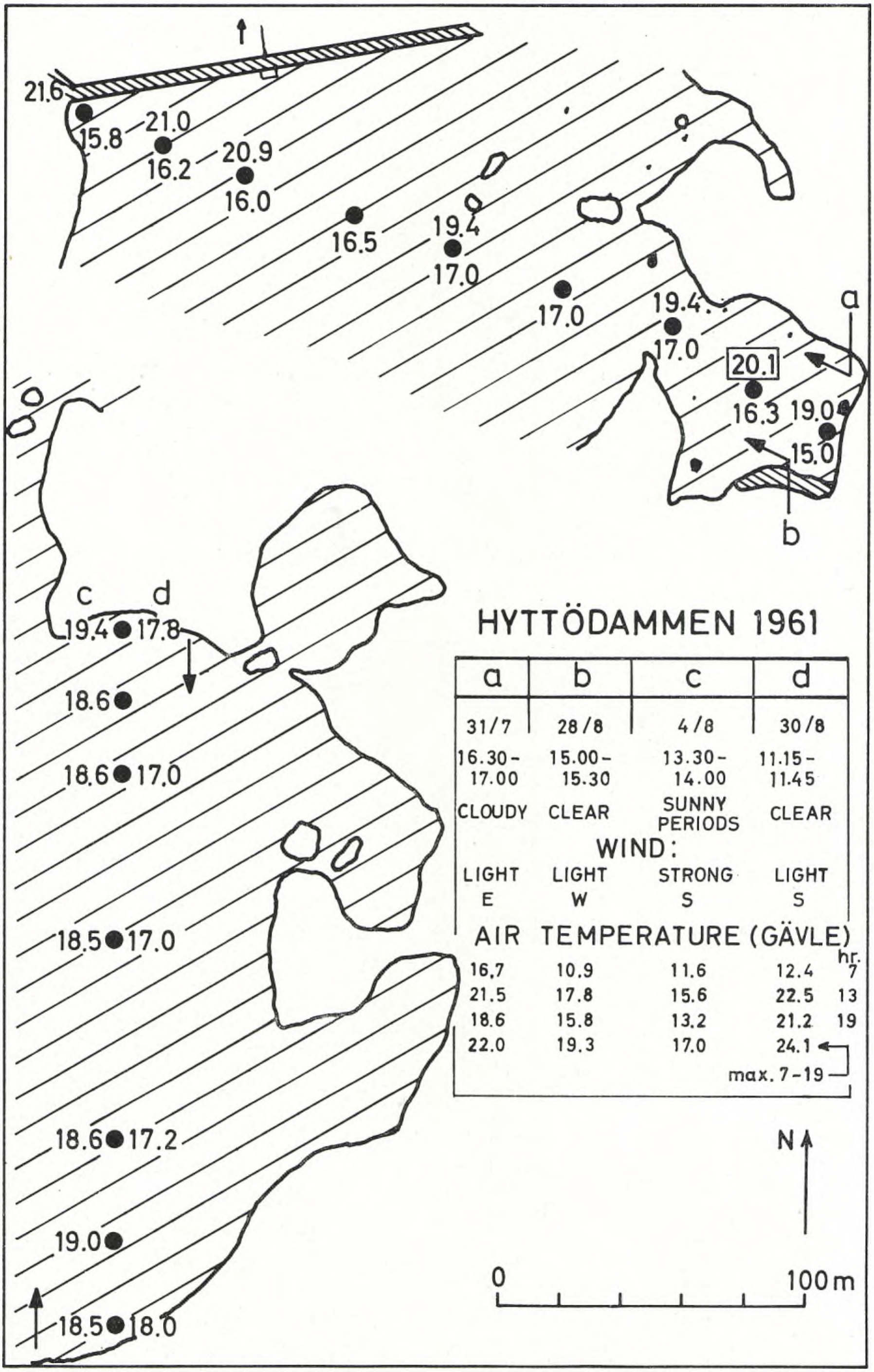
			Dalälv	1	2	3	4 a	4 b	4 c	Outlet
1960	May	13	—	—	—	—	16.4	—	—	—
		14	—	14.0	—	—	—	—	—	—
		26	—	—	15.6	15.0	15.8	15.9	15.9	—
	June	6	—	20.0	22.7	23.4	24.0	23.6	20.0	—
		13	—	18.4	19.8	19.5	19.0	18.8	18.8	—
		18	18.8	18.9	20.7	20.5	20.6	20.2	19.2	—
		28	—	18.6	19.4	19.2	19.4	19.7	19.1	—
	July	2	17.5	18.7	18.7	19.7	19.6	19.1	18.3	—
		9	—	18.4	19.1	19.3	19.5	18.7	17.9	—
		19	—	18.0	19.0	18.9	19.2	19.2	19.1	—
		27	—	18.1	18.7	19.2	19.6	19.3	18.6	—
	Aug.	2	—	20.9	22.5	24.1	23.3	21.2	19.6	—
		8	—	17.6	17.9	17.8	18.1	18.1	17.8	—
		17	—	16.1	17.2	16.7	17.8	17.1	16.9	—
		23	—	15.8	15.8	16.0	16.1	16.0	15.8	—
		31	—	13.9	15.0	15.3	15.8	15.5	14.8	—
	Sept.	6	—	15.8	15.8	16.0	16.1	16.0	16.0	—
		12	—	13.8	13.5	13.6	13.9	13.5	12.8	—
		20	—	14.2	14.1	14.2	14.4	14.3	13.8	—
		28	—	9.5	7.5	7.8	8.5	8.5	8.5	—
	Nov.	7	2.8	—	—	—	—	—	—	—
	Dec.	19	—	—	—	—	—	—	—	1.3
1961	Feb.	11	—	—	—	—	0.5	2.0	—	—
	Mar.	30	—	—	—	—	3.6	—	—	3.8
	Apr.	8	—	—	—	—	4.3	—	—	—
		29	9.5	—	—	—	—	—	—	9.9
	May	22	11.9	13.1	14.1	14.4	14.3	14.1	13.5	—
		30	—	11.2	11.1	11.1	11.7	11.6	11.3	—
	June	7	18.9	19.3	22.3	22.3	22.6	22.6	18.7	—
		14	—	18.7	19.7	19.6	20.3	20.1	19.5	—
		20	—	16.3	17.2	16.9	17.3	17.1	16.7	—
		26	—	17.3	18.9	19.0	18.3	17.5	17.1	—

Table 2. Continued.

			Dalälv	1	2	3	4 a	4 b	4 c	Outlet
	July	4	—	18.3	20.2	19.7	20.0	20.0	18.0	—
		10	—	18.6	18.7	19.3	19.0	18.9	18.3	—
		18	—	21.1	22.7	22.6	22.1	22.0	20.4	—
		24	—	18.4	18.7	18.9	18.5	17.9	17.4	—
		26	17.4	17.4	17.4	17.5	18.0	—	17.8	17.7
		31	—	19.3	21.4	21.2	21.1	20.0	18.0	—
	Aug.	7	—	16.2	16.9	17.2	17.3	17.3	16.6	—
		14	—	17.7	19.2	18.3	18.5	18.2	17.5	—
		15	16.6	16.6	17.2	16.9	17.4	—	17.2	17.4
		21	—	14.3	15.4	15.7	15.2	14.9	14.7	—
		28	—	14.2	14.8	14.5	15.7	15.2	14.3	—
	Sept.	1 [1]	—	—	—	—	16.5	16.1	15.4	—
		1	—	—	—	—	17.1	16.6	15.6	—
		1	—	—	—	—	18.2	16.5	15.5	—
		1	—	—	—	—	17.9	16.8	15.8	—
		1	—	—	—	—	17.1	17.0	16.0	—
		2	—	—	—	—	16.5	16.8	15.6	—
		4	—	14.5	14.9	14.8	15.2	15.2	15.1	—
		5	14.6	14.4	14.0	14.0	14.7	—	14.6	—
		11	—	13.4	13.1	13.1	13.1	13.0	12.8	—
		17	—	15.2	16.1	16.5	15.0	14.5	14.2	—
		23	14.6	14.5	14.3	13.9	14.1	13.0	12.7	13.6
	Oct.	3	—	12.4	12.0	12.2	12.1	12.1	12.1	—
		8	—	11.6	11.1	11.1	11.4	11.2	11.2	—
	Nov.	1	7.4	7.3	6.1	6.3	6.4	6.4	6.4	6.4
		8	—	4.4	3.4	3.3	2.8	2.8	2.6	—
	Dec.	4	—	1.8	1.4	1.0	1.0	—	—	—
		19	—	1.5	1.2	—	0.3	—	—	—
1962	Jan.	15	—	—	—	—	0.5	0.5	0.5	—
		26	—	—	—	—	0.4	0.4	0.4	—
	Mar.	13	—	0.4	0.4	—	0.2	0.2	0.2	—
	Apr.	10	—	—	—	—	0.7	0.8	0.9	—
	June	8	—	—	17.6	17.6	17.6	17.6	17.6	—
		13	13.7	14.0	16.1	16.2	16.5	—	15.7	16.1
		18	—	—	—	—	20.5	—	18.6	—
		21	—	15.8	18.0	17.5	18.2	18.2	18.2	—
		27	—	15.7	17.3	17.1	17.4	17.4	17.3	—
	July	3	—	16.1	17.7	—	18.1	18.2	17.5	—
		11	—	16.0	17.1	17.3	17.3	17.1	17.0	—
		25	—	17.2	18.2	18.4	18.0	17.8	17.3	—
		29	—	—	—	—	20.4	—	18.0	—
	Aug.	8	16.3	16.0	16.4	16.3	16.7	17.1	17.1	16.7
		14	—	15.2	15.7	16.2	16.0	15.8	15.7	—
		21	—	18.8	19.2	20.0	19.2	17.3	16.6	—
		27	—	—	14.2	—	14.5	—	14.6	—
	Sept.	4	—	13.6	13.6	13.7	13.6	13.5	13.1	—
	Oct.	10	—	9.6	9.4	9.5	10.1	9.5	9.5	—
		24	6.0	6.0	5.6	5.7	5.8	—	5.6	—
	Nov.	26	—	0.6	1.8	1.6	1.3	—	1.2	—

[1] Measurements at 1/9—2/9 at the following times of day: 0600, 1000, 1500, 1800, 2200, 0200.

From Fig. 5 it can be shown that the water becomes warmer than the air. This was shown by NEESS and BUNGE (1956) in their examination of BIRGE's unpublished temperature data. The higher temperature of the water as compared with that of the air is due to conversion of radiation energy to heat



HYTTÖDAMMEN 1961

a	b	c	d	
31/7	28/8	4/8	30/8	
16.30- 17.00	15.00- 15.30	13.30- 14.00	11.15- 11.45	
CLOUDY	CLEAR	SUNNY PERIODS	CLEAR	
WIND:				
LIGHT E	LIGHT W	STRONG S	LIGHT S	
AIR TEMPERATURE (GÄVLE)				hr.
16,7	10.9	11.6	12.4	7
21.5	17.8	15.6	22.5	13
18.6	15.8	13.2	21.2	19
22.0	19.3	17.0	24.1	max. 7-19

Fig. 6. Temperature data showing horizontal transport of water in the parts of the pond with sparse higher plant vegetation.

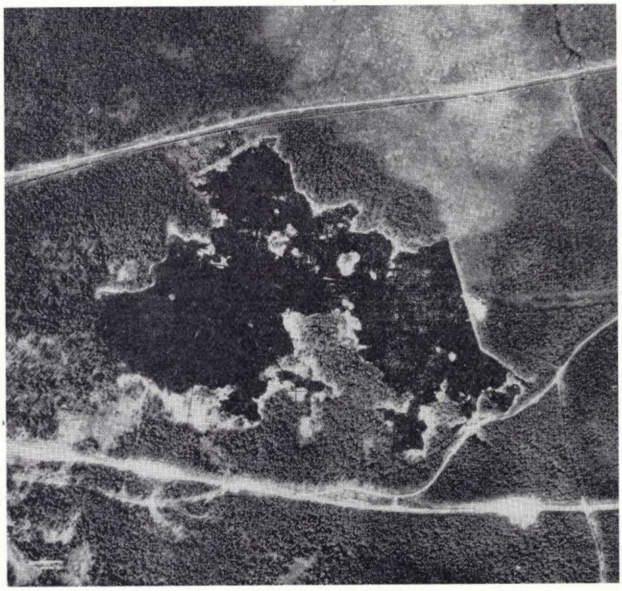


Fig. 7 a.

Fig. 7 b.

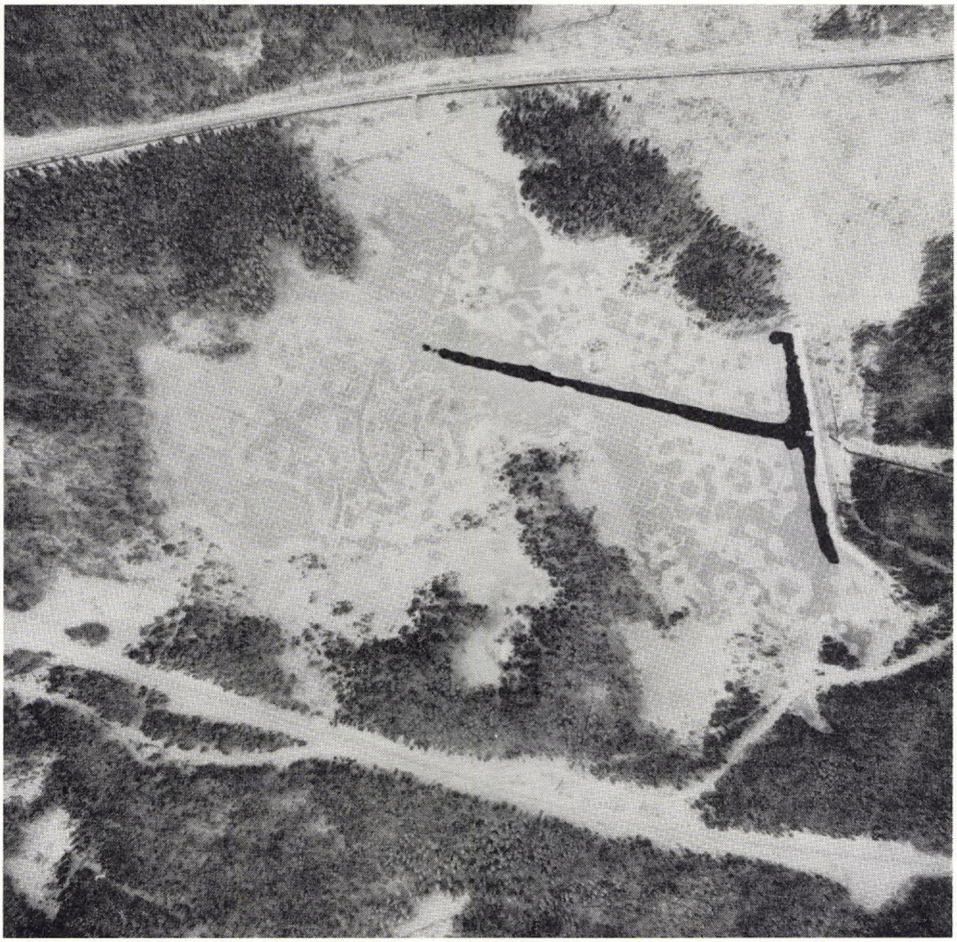


Fig. 7 c.

Fig. 7 a—c. Air photographs. Published by permission of Försvarsstaben, Stockholm. (a) 17/6 1963; showing the pond before the higher plant vegetation had grown up, (b) 7/8 1962, the same after the higher plant vegetation had grown up, (c) 27/11 1962, showing the pond frozen except above the aeration tube.

energy. It must be remembered that the temperature was measured at Gävle, which means somewhat cooler temperature than at Hyttödammen in the early summer, but the differences are too large to be explained by this alone.

Comparing 1961 and 1962 in Fig. 5, as the sum of the daily temperatures during the period June 1—Oct. 15, it is apparent that 1961 was slightly warmer than 1962. This can be directly correlated with the sums of air temperature which were 1,900 for 1961 and 1,660 for 1962. The corresponding values for the water are 2,290 and 2,210, respectively, and the two years differ mainly in the conditions in the first half of June.

Examples of the horizontal transport of water by wind can be taken from the northern part of the pond with sparse vegetation: easterly and westerly winds predominate. In the other parts no safe interpretation of the temperature data from the different sampling occasions can be made, other than in the SE bay, when northerly or southerly winds were prevalent. Sampling has most often taken place in such directions as not to correspond with any wind direction. The temperature values from a number of different observations are presented in Fig. 6. The measurements were made with a Ruttner-sampler thermometer at a depth of 0.5 m at all the sites. The arrows show the direction of travel and the order in which the samples were taken. The Figure shows that a certain water transport can occur under suitable conditions in the north part of the pond but not in the SE bay during the vegetation period, indicating that the vegetation strongly reduces the effect of the wind. The distribution of the vegetation is given by ARNEMO and NORLIN (1962) and by the aerial photographs (Fig. 7) which were taken before the vegetation had grown up (June 17 1963) and during the time of its greatest development (Aug. 7 1962). Figure 6 also shows that the water warms up more near the land in the SE bay than further out independently of the wind direction.

An example of how much the water can warm up during a sampling series is given by the data from July 31 1961 in Fig. 6. Sampling began in the east end and when it was finished the temperature was measured at the site which has been marked out by framing the temperature value (Fig. 6). In half-an-hour the temperature rose about $^1/_2$° C.

Vertical temperature stratification occurs in the pond but rarely persists for long during the summer. This is shown in Table 2, where the temperature at site 4 is given. I have not performed any regular studies of the diurnal temperature cycle so as to prove this, but WEIMANN (1933, 1935) reports from his pond investigations circulation during summer due to lower night air temperatures. The phenomenon of this circulation forms essential differences in physical and chemical conditions when comparing ponds with lakes. Very good studies on pond function and production are given in the works by WEIMANN (1933, 1935, 1942). Furthermore, MEGARD (1961) has studied the diurnal interactions between some environmental factors and production.

During the winter there was no stratification because of the movement of the whole water mass resulting from the aeration with the bubble tube. The temperature falls slowly during the winter as a consequence of a rapid cooling in connection with the exposure of the water to the cold air at the ice-free surface above the bubble tube. The water's lowest temperature, 0.2°, occurred on March 13 1962.

Simultaneous measurements to show principal differences in temperature between areas with and without vegetation have not been made. The conditions in the littoral zone of lakes differ from those of the profundal zone in the temperature of the bottom water (PUKE 1949). GIEYSZTOR (1961), in an investigation of differences in water chemistry and temperature between open water and the littoral zone in a lake, suggested that the littoral conditions can change depending on the vegetation. This applies not only to the quantity of the vegetation but also to its composition.

2. Transparency

Transparency varies between 180 cm and a value larger than can be measured at the pond's deepest point, where all the measurements were taken. The transparency values from the summers of 1961 and 1962, in Fig. 8, indicate that the pond water was generally more transparent in 1962 than in 1961. The values from autumn 1962 show effects of turbidity, caused by dredging in the Dalälv in the neighbourhood of the upper end of the flume.

3. Colour

Colour values are shown in Figs. 9 and 10. They vary between 30 (March 30 1961) and 75 (May 18 1962 and Oct. 23 1962) mg Pt/l. No significant differences in the variation between the different sites seem to occur.

4. Oxygen

The oxygen content shows no large variation during the summer. The values lie mostly grouped between 90 % and 110 % of saturation with the largest value of 173 % on July 31 1961 and the smallest of 58 % on Sept. 4 1961; see Fig. 11 a and b.

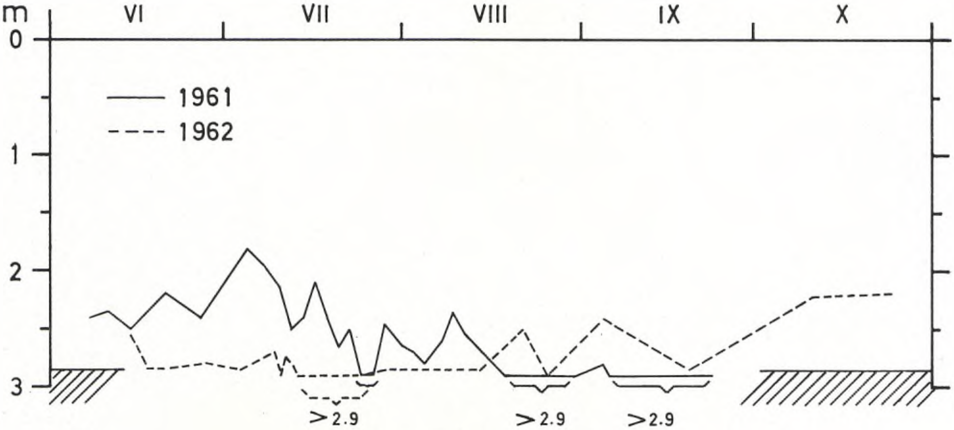


Fig. 8. Transparency at S (Fig. 2).

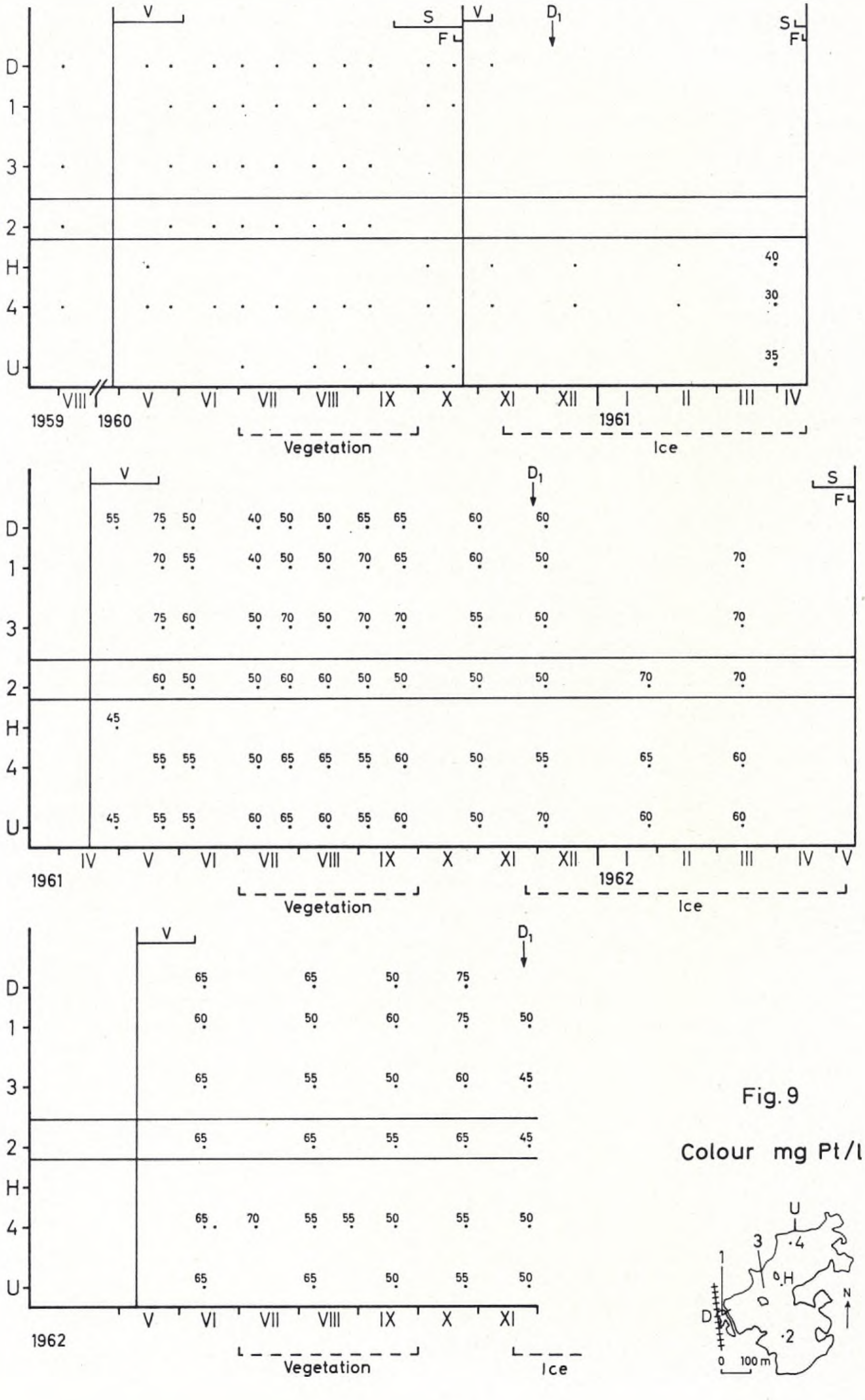


Fig. 9

Colour mg Pt/l

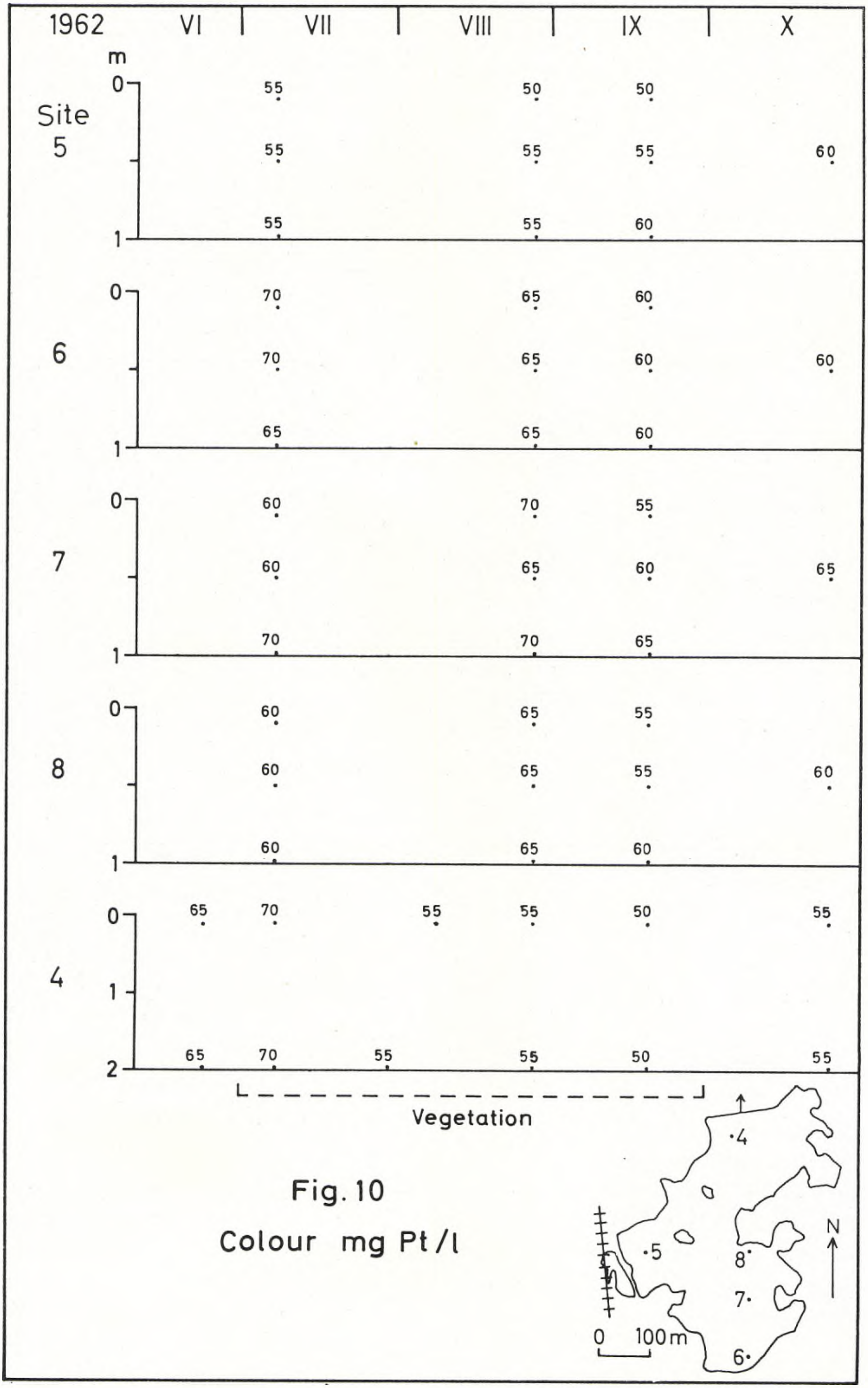


Fig. 10

Colour mg Pt / l

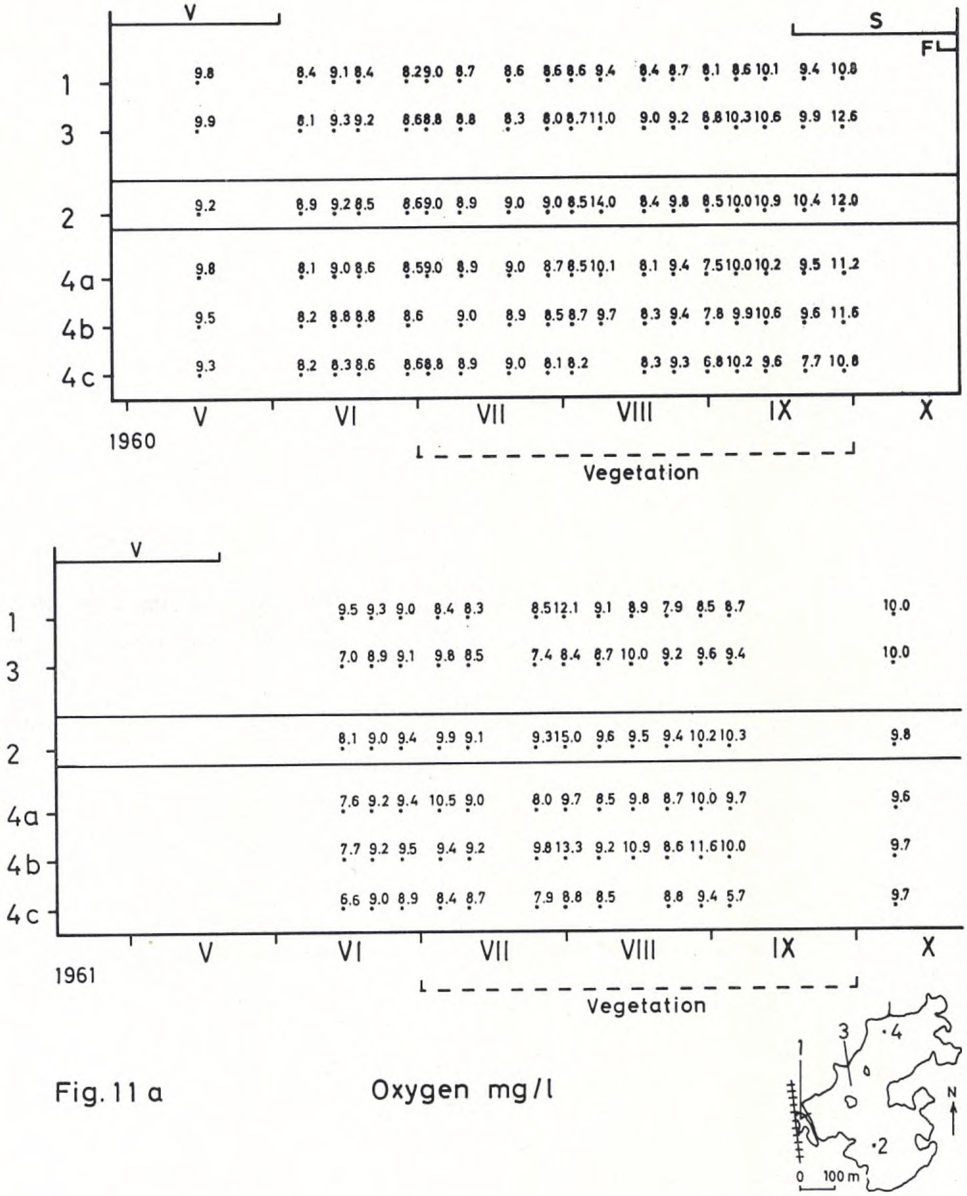


Fig. 11 a Oxygen mg/l

In the summers of 1957 and 1958 STEFFNER studied the daily variation at different sites in the pond (reported in his annual report to the Fishery Board). He found that the saturation percentage of oxygen was as a rule 90—100 with the exception of the bottom water directly in front of the outlet, which varied between 50 % and 80 % on June 17—18 1957. No significant variations in either the horizontal or the vertical plane were noted.

STEFFNER (pers. comm.) has also given an account of the oxygen condi-

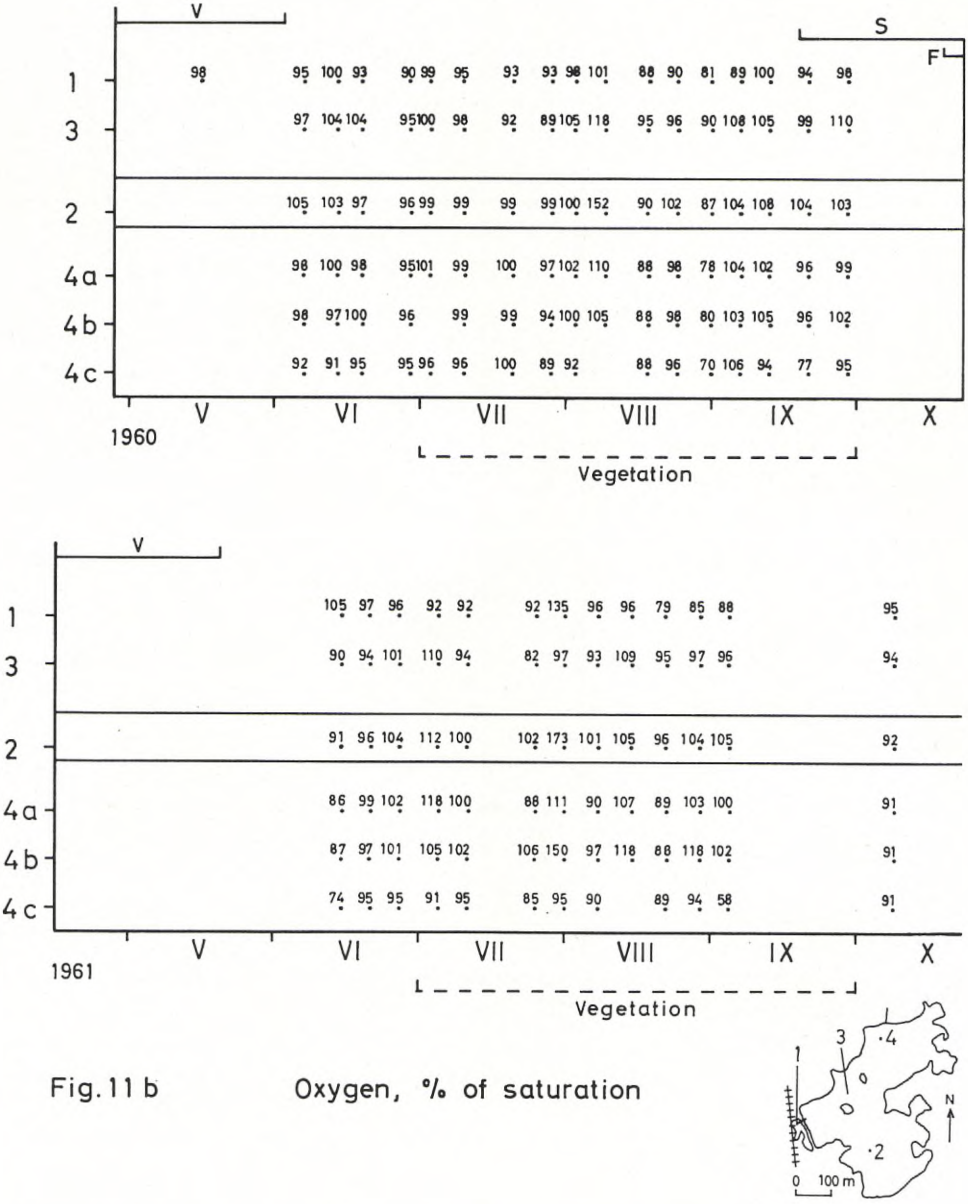


Fig. 11 b Oxygen, % of saturation

tions during the winters in which the pond was water-filled. The oxygen content was low, especially in the area where the water was not aerated, and it was improved by aeration. During the most critical period there was, in the aerated part of the pond, an area about 1 m from the aerated part with 78 % of saturation as the highest value. The lowest value at the same time was 2 %, occurring 150 m from the end of the bubble tube, where the degree of saturation was 14 %.

5. pH

The pH varies mainly around 7, as is shown in Figs. 12 and 13. A line has been drawn for pH 7. In September 1960 and September 1961 the lowest values, 6.40, were recorded. The highest value, 8.55 (one further value, 8.20, is above pH 8) was recorded at the end of April 1961. These are probably temporary peaks caused by phytoplankton photosynthesis. No constant differences between different parts of the pond could be found. Judging from observations in 1962, pH at site 6 may be different from the others. The pH was never less than 7. However, the pH of the spring water varied during the winter between 6.70 and 7.40, and is thus slightly different from the values for site 6. The series of samples taken on July 31 and Aug. 4 1961, designed to study possible horizontal heterogeneity in the pond, show that there was a pH increase in the south-eastern part of the SE bay (see Fig. 14 a and b). In other parts of the pond there were no pronounced tendencies. It must be emphasized that the small quantity of data allows no general conclusions.

6. Specific conductivity

Figs. 15 and 16 show the variation in specific conductivity. At the time of filling with spring water, in March—May, the water has a high $\varkappa$-value of $100—200 \cdot 10^{-6}$ (see Fig. 2 for situation and p. 41 for ionic composition). The mean of 26 measurements of spring water, varying between 141 and $345 \cdot 10^{-6}$ was $255 \cdot 10^{-6}$. When the pond is afterwards kept filled with additions of Dalälv water, $\varkappa$ is about $50 \cdot 10^{-6}$. The $\varkappa$-value for Dalälv water, from the few analyses from the short period during which filling takes place, varies between 35 and $45 \cdot 10^{-6}$. For May 15 1960 a value of $61 \cdot 10^{-6}$ was recorded, but this can be explained by the fact that the sample was taken on the first day on which water ran through the flume, which is partly of wood and partly a channel excavated in the soil. This had been dry during the winter. LOHAMMAR (1949) and AHL (1964) showed that sulphate content increases in surface run-off water after a long drying-out period. Oxidation processes similar to those which take place in soil and lead to increased leaching out of sulphate would be expected to take place, in those parts of the flume that consist of channels excavated in the soil, when water is not running through. The high values observed probably sink rapidly to those of the Dalälv water entering the flume. After the filling of the pond, $\varkappa$ varies somewhat from year to year depending on the amount of spring water used for filling before the Dalälv water is let in. After the pond is full, $\varkappa$ decreases in the different sites because water is then added to a much greater extent from the Dalälv than from the springs. The incoming water is well mixed throughout the pond before the higher vegetation develops. (See Fig. 17 b for the situation on June 14 1962.)

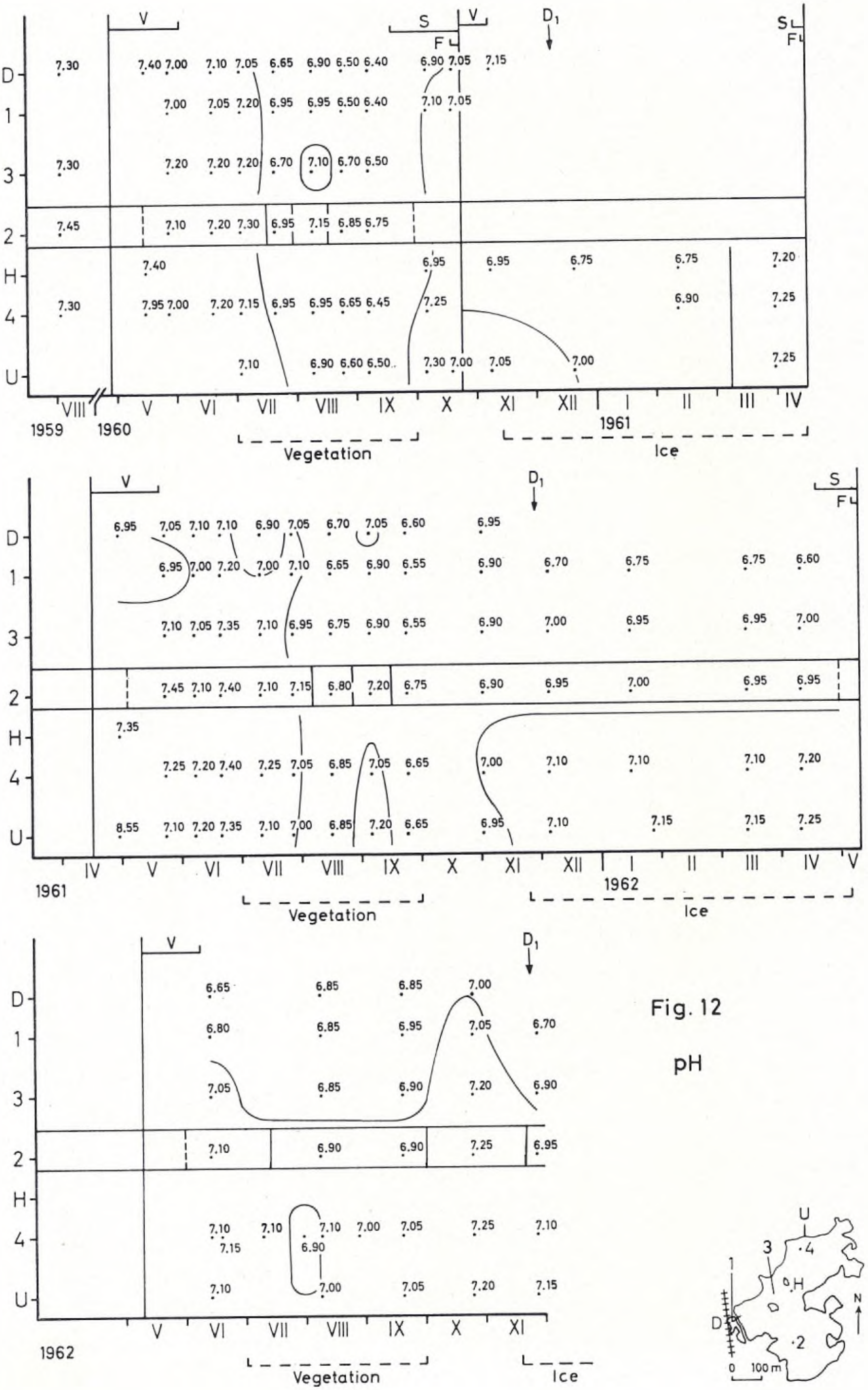
When the vegetation has grown up, it hinders mixing, mainly between the SE bay and the other parts of the pond (see p. 83—85). The mixed water from the Dalälv and the springs then gives a large part of the pond a ϰ-value 10—15 units higher than that of the incoming Dalälv water. This is exemplified by the situation on July 16 1962 in Fig. 17 b. After that, horizontal heterogeneity builds up in the SE bay. This is more or less pronounced in different years, as is shown by a comparison between the situations in Fig. 17 a and b on Aug. 4 1961 and Aug. 2 1962, and on Sept. 11 1961 and Sept. 19 1962, and this depends on variation in the flow of the springs. Note also in Fig. 15 that the 50 isoplete is reached earlier at site 2 than at the other sites. Another factor relevant in this connection, and of importance for small volumes of water like Hyttödammen, is the precipitation and evaporation in different years. The significance of these conditions cannot be estimated, since no information is available for a comparison of evaporation in the summers of 1961 and 1962.

After the *Sagittaria* has died down, the horizontal heterogeneity can be broken up by the effect of the wind. See Fig. 17 a, Oct. 8 and Nov. 8 1961. After that there is a slow increase of ϰ through mixing with spring water. (See Fig. 17 a, Dec. 4 1961.)

A more detailed picture of the pattern described above is obtained from Fig. 16. Before the vegetation grows up, only the bottom water at site 6, in the immediate vicinity of the springs, shows any difference from other sites. After the vegetation has grown up, site 5 is influenced solely by Dalälv water, while sites 6, 7 and 8 are influenced in decreasing degrees by the spring water, in terms of distance and time. At site 4 there is mixed water from the two sources. Judging from the conductivity values, the spring water is already mixed vertically with the other water in the pond between sites 6 and 7. One reason for this is that fishing with a seine net takes place continuously within the area. After the dying down of the vegetation, the pond shows no noteworthy horizontal heterogeneity, according to samples taken in October as mixed samples from the complete vertical water profile.

The horizontal heterogeneity observed during the summer has no similarly pronounced equivalent in the winter. The ice might then be thought to have the same effect as the vegetation and prevent mixing. But because the ice reduces the volume of the free water very considerably through successive formation through the whole of the winter (see p. 8) the specific conductivity is raised by concentration alone, through the freezing effect, so much that the effect of the springs largely disappears. However, the higher values recorded on Jan. 15 and March 13 1962 (Fig. 17 a) in the SE bay are probably due to the influence of the spring. On the Dalälv side of the pond, with a similar depth, no similar increase could be observed.

The situation on Apr. 10 1962 (Fig. 17 a) showed a clear influence of melt water. On this occasion the ice was thawing.


V
S
F
V
D1
S
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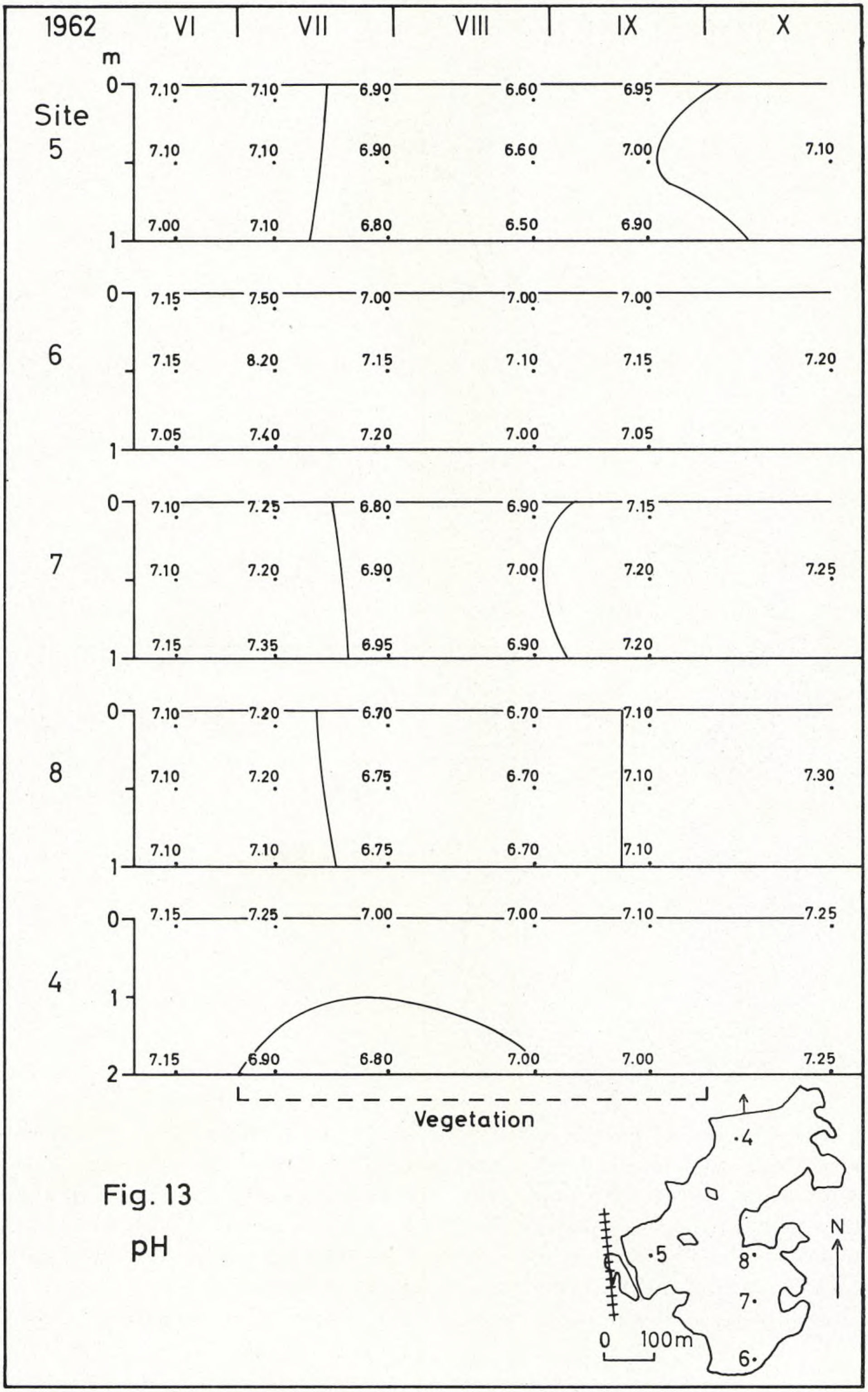
D
1
3
2
H
4
U
7.30 7.40 7.00 7.10 7.05 6.65 6.90 6.50 6.40 6.90 7.05 7.15
7.00 7.05 7.20 6.95 6.95 6.50 6.40 7.10 7.05
7.30 7.20 7.20 7.20 6.70 7.10 6.70 6.50
7.45 7.10 7.20 7.30 6.95 7.15 6.85 6.75
7.40 6.95 6.95 6.75 6.75 7.20
7.30 7.95 7.00 7.20 7.15 6.95 6.95 6.65 6.45 7.25 6.90 7.25
7.10 6.90 6.60 6.50 7.30 7.00 7.05 7.00 7.25
VIII V VI VII VIII IX X XI XII I II III IV
1959
1960
1961
Vegetation
Ice
V
D1
S
F
6.95 7.05 7.10 7.10 6.90 7.05 6.70 7.05 6.60 6.95
6.95 7.00 7.20 7.00 7.10 6.65 6.90 6.55 6.90 6.70 6.75 6.75 6.60
7.10 7.05 7.35 7.10 6.95 6.75 6.90 6.55 6.90 7.00 6.95 6.95 7.00
7.45 7.10 7.40 7.10 7.15 6.80 7.20 6.75 6.90 6.95 7.00 6.95 6.95
7.35
7.25 7.20 7.40 7.25 7.05 6.85 7.05 6.65 7.00 7.10 7.10 7.10 7.20
8.55 7.10 7.20 7.35 7.10 7.00 6.85 7.20 6.65 6.95 7.10 7.15 7.15 7.25
IV V VI VII VIII IX X XI XII I II III IV V
1961
1962
Vegetation
Ice
V
D1
6.65 6.85 6.85 7.00
6.80 6.85 6.95 7.05 6.70
7.05 6.85 6.90 7.20 6.90
7.10 6.90 6.90 7.25 6.95
7.10 7.15 7.10 6.90 7.10 7.00 7.05 7.25 7.10
7.10 7.00 7.05 7.20 7.15
V VI VII VIII IX X XI
1962
Vegetation
Ice
U
3
4
1
H
D
2
N
0 100 m

Fig. 12

pH


1962
VI
VII
VIII
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X
m
Site
5
0
1
7.10 7.10 6.90 6.60 6.95
7.10 7.10 6.90 6.60 7.00 7.10
7.00 7.10 6.80 6.50 6.90
6
0
1
7.15 7.50 7.00 7.00 7.00
7.15 8.20 7.15 7.10 7.15 7.20
7.05 7.40 7.20 7.00 7.05
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7.10 7.20 6.70 6.70 7.10
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7.15 7.25 7.00 7.00 7.10 7.25
7.15 6.90 6.80 7.00 7.00 7.25
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100m

Fig. 13

pH

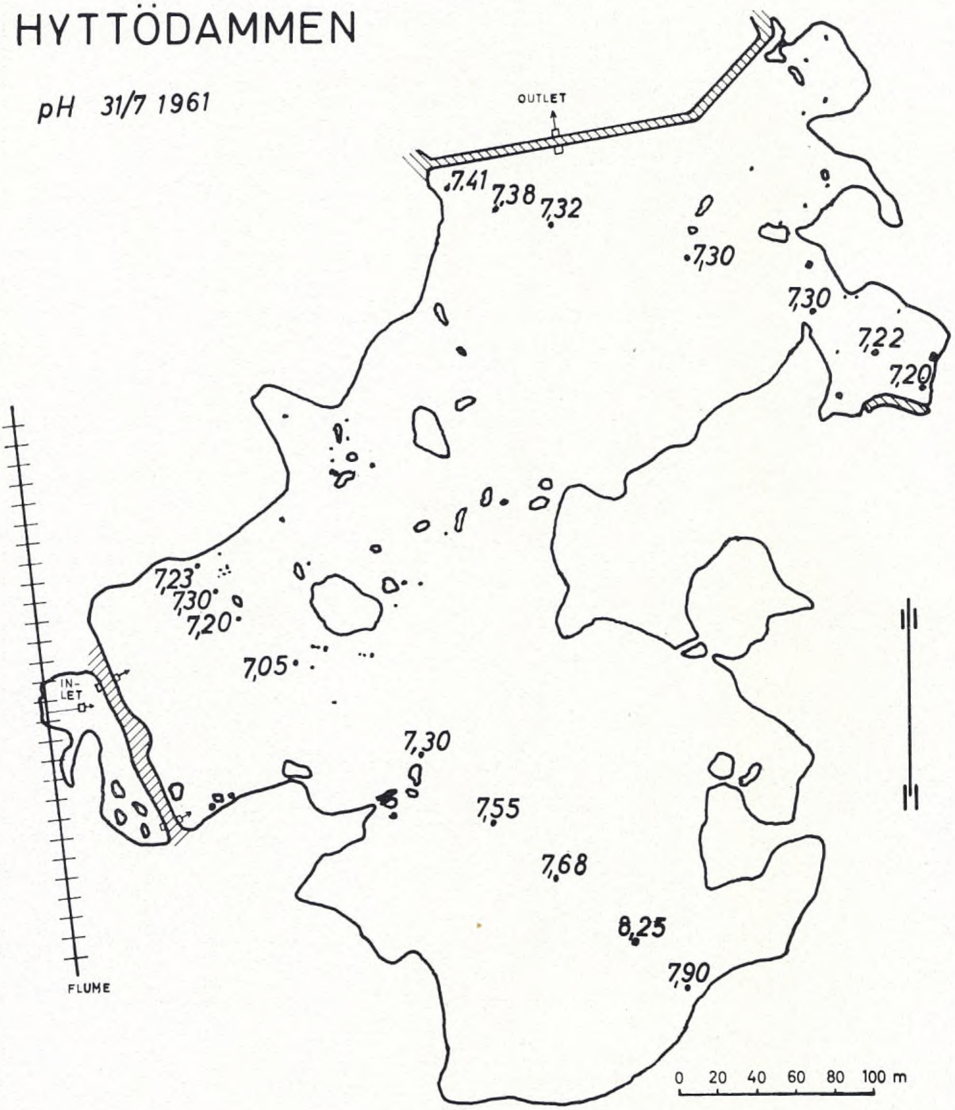


Fig. 14 a.

The flow of the springs in the pond varies from year to year. Sometimes a spring may actually dry up, and sometimes a new one may appear. To judge from observations made when the pond was dry, the most important flow is that from three springs, very close together, in the SE bay (See Fig. 2, where they are shown as one point). These flows are more or less wholly responsible for the horizontal heterogeneity described above. However, in other sites local conditions for heterogeneity caused by spring water, a form

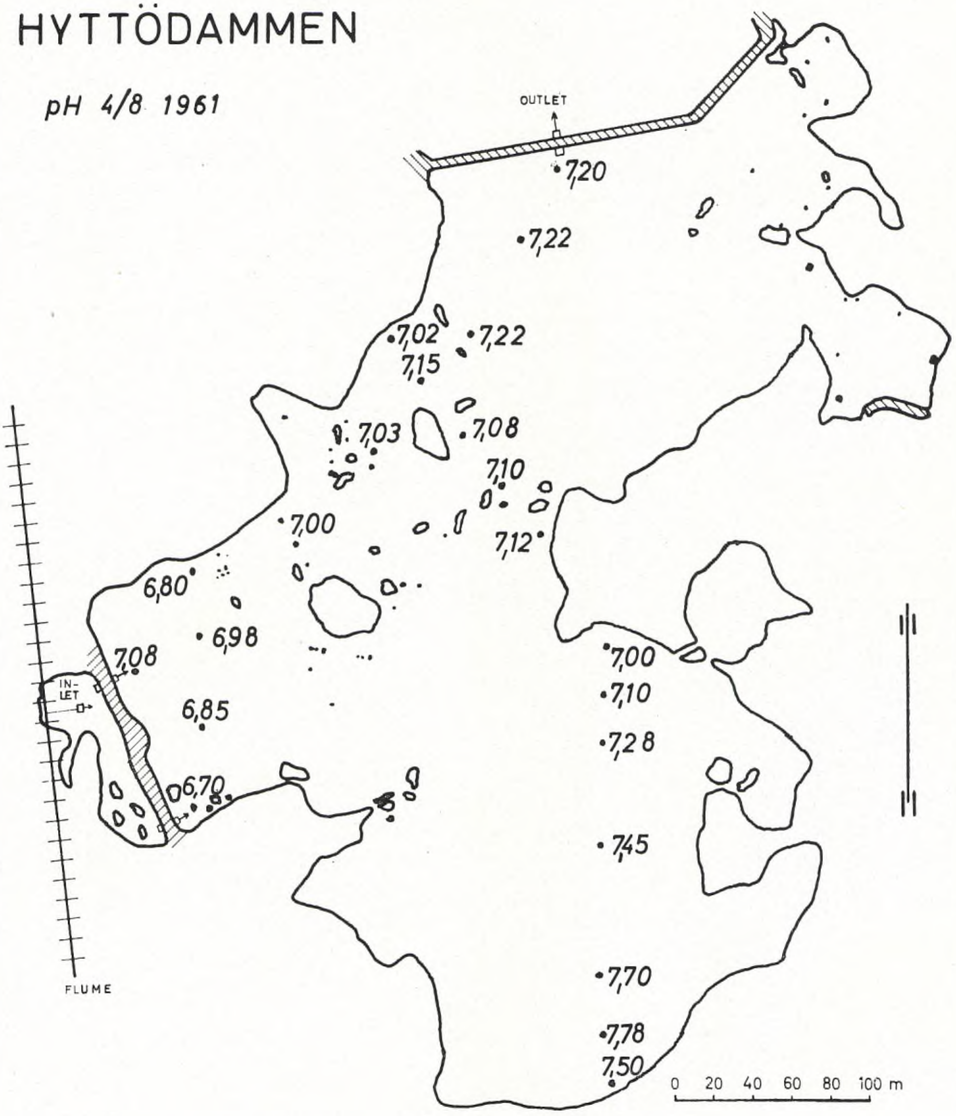
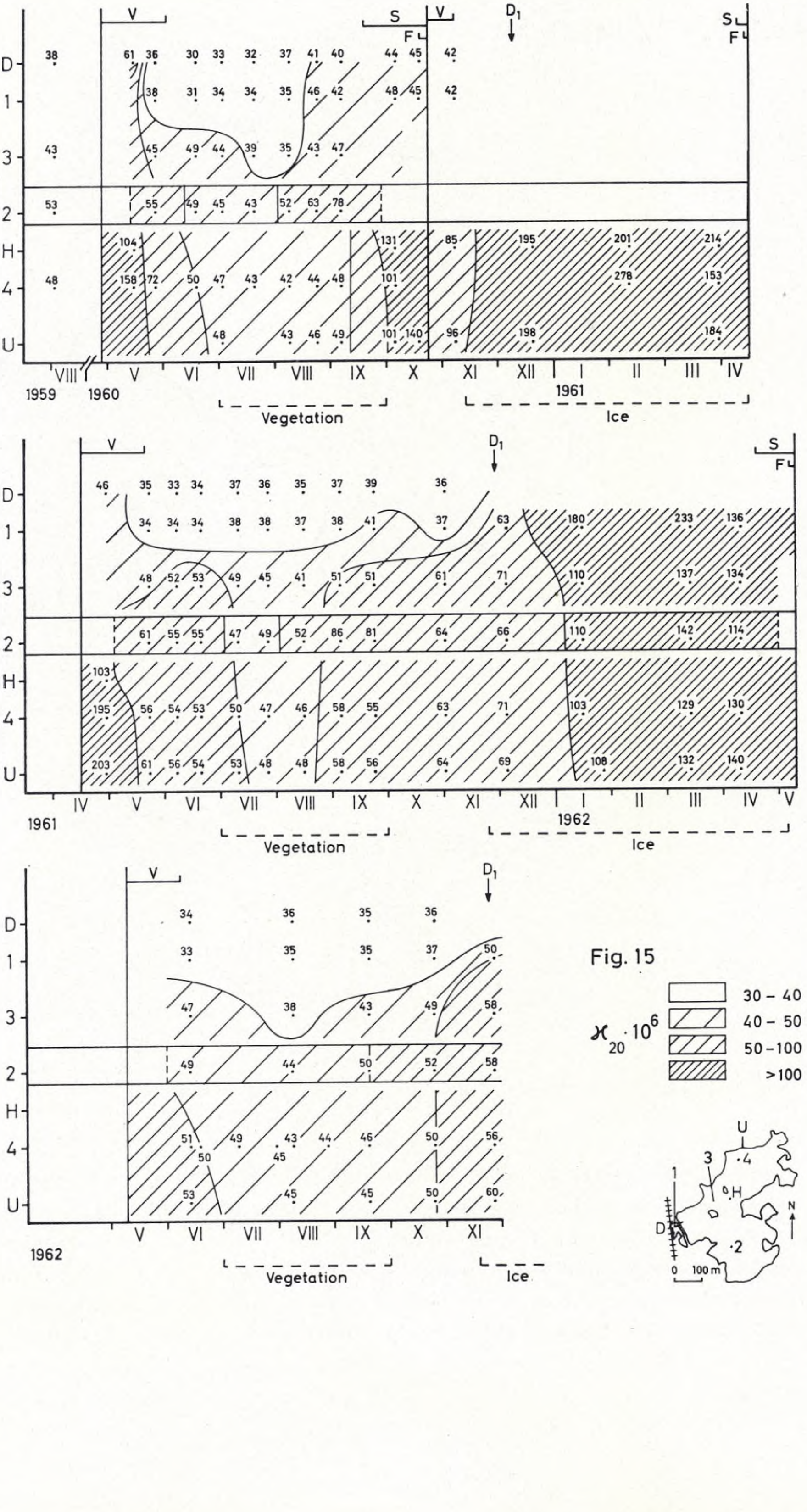


Fig. 14 b.

Fig. 14 a and b. Horizontal distribution of pH. (a) 31/7 1961, (b) 4/8 1961.

of microclimate, certainly occur. For example, $\varkappa$ for site 1 on 15 sampling occasions was larger than, on 4 the same as, and on 4 less than that of Dalälv water. Since change of the water mass is rapid in the small pond, between the flume and the pond itself, where site 1 is situated, the flow of another source of water must be large compared with the inflow of Dalälv water in order to have any considerable effect. Therefore the spring water flowing


D
1
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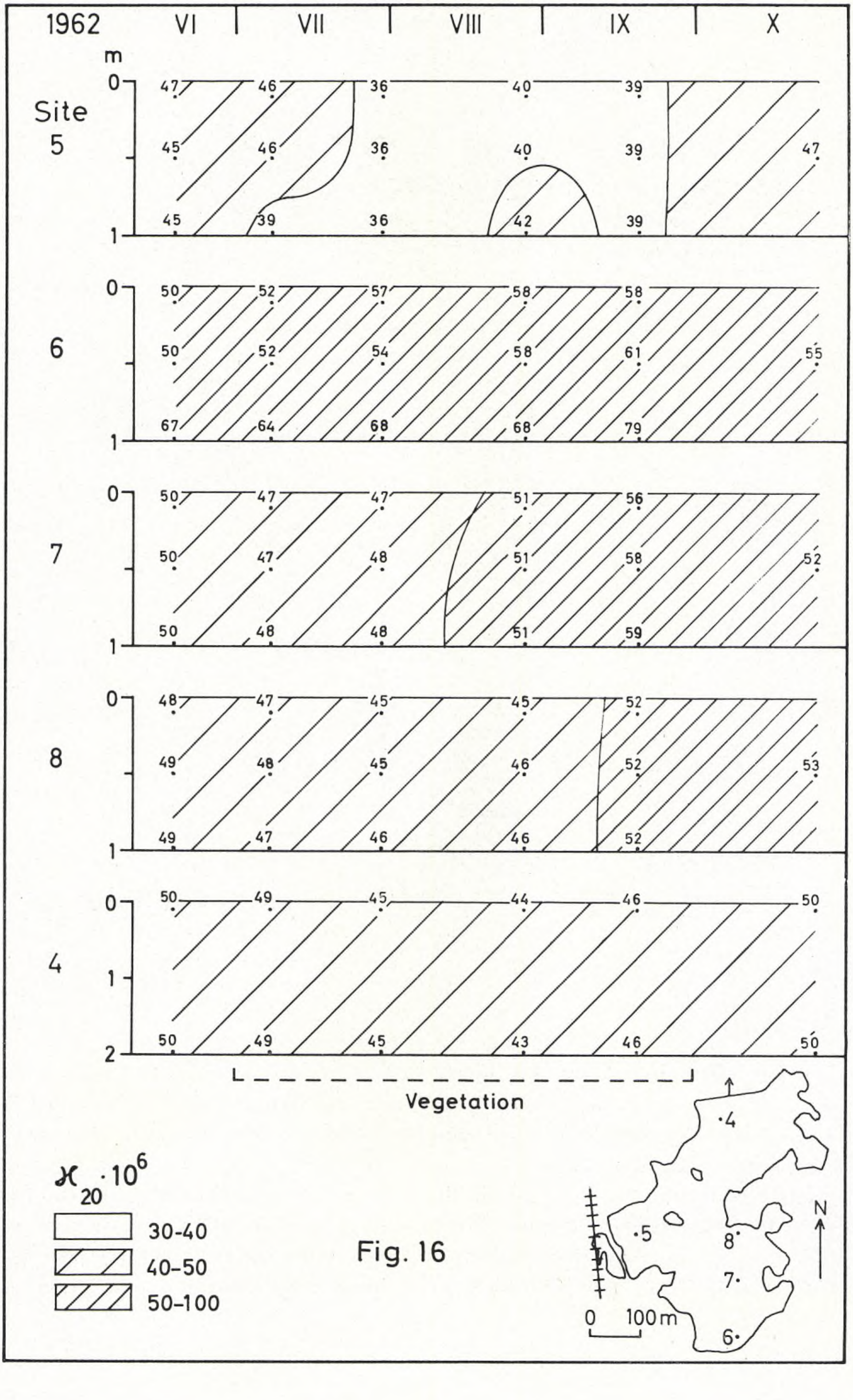
D1
VIII
V
VI
VII
VIII
IX
X
XI
XII
I
II
III
IV
1959
1960
1961
1962
Vegetation
Ice
30 – 40
40 – 50
50–100
>100
ϰ20 · 10^6
N
0
100 m

Fig. 15


1962
VI
VII
VIII
IX
X
m
Site 5
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47 46 36 40 39
45 46 36 40 39 47
45 39 36 42 39
6
0
1
50 52 57 58 58
50 52 54 58 61 55
67 64 68 68 79
7
0
1
50 47 47 51 56
50 47 48 51 58 52
50 48 48 51 59
8
0
1
48 47 45 45 52
49 48 45 46 52 53
49 47 46 46 52
4
0
1
2
50 49 45 44 46 50
50 49 45 43 46 50
Vegetation
$\varkappa_{20} \cdot 10^6$
30-40
40-50
50-100
·4
·5
8·
7·
6·
N
0 100 m

Fig. 16

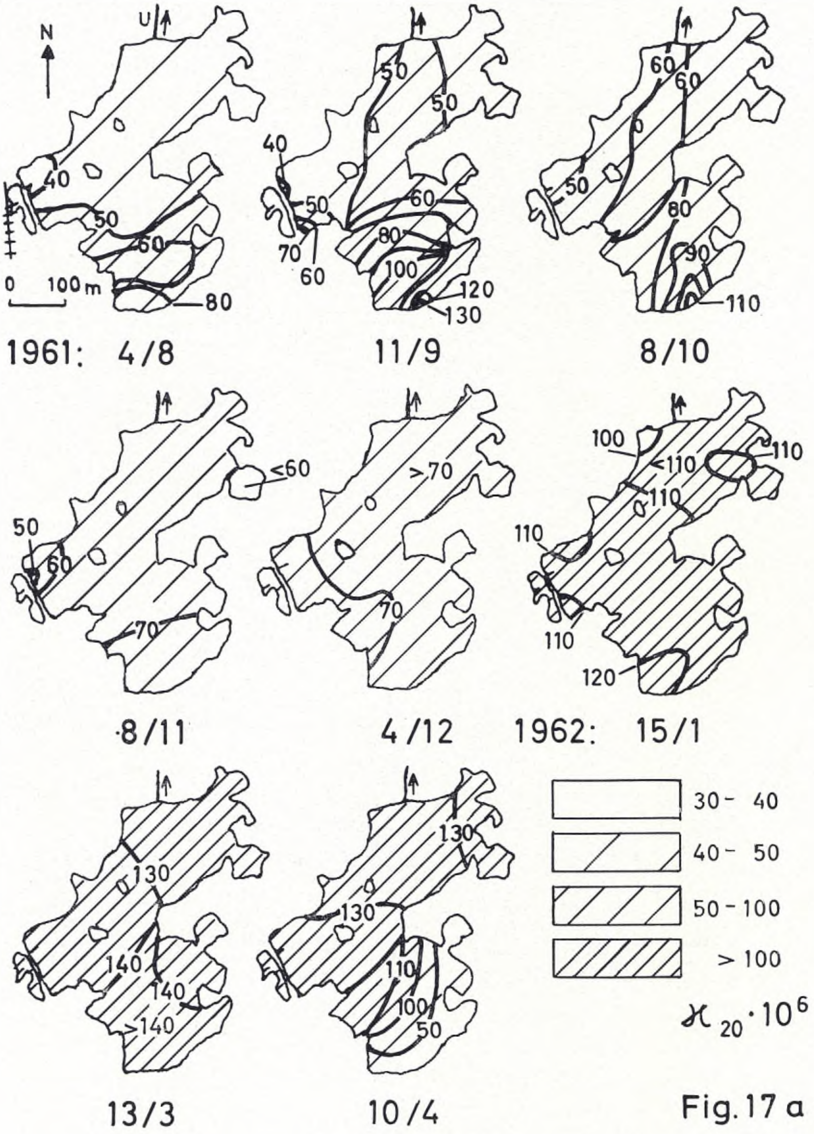
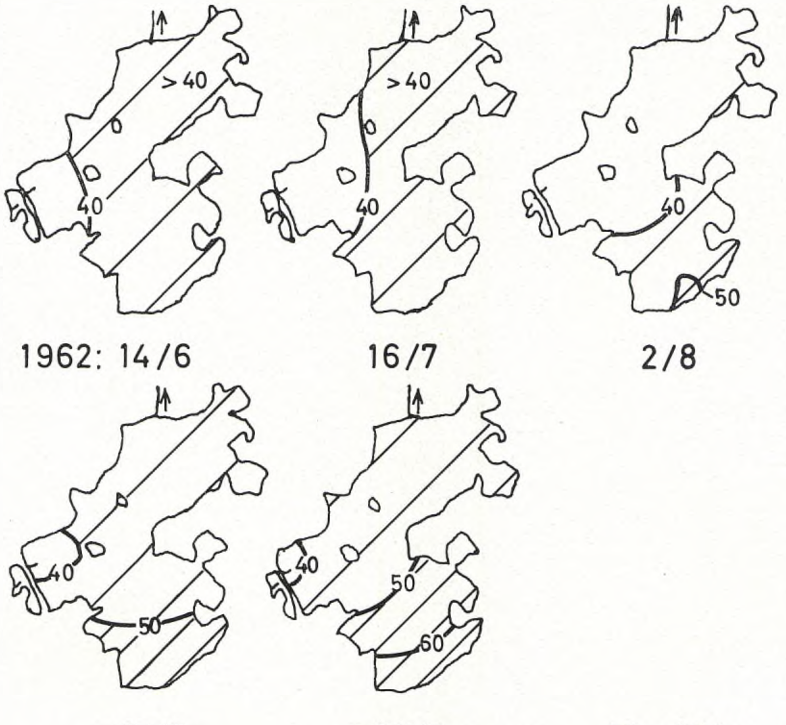


Fig. 17 a

in at the southern end of the upper part of the pond cannot significantly increase the ϰ value. Besides, the small increases which have been recorded can perhaps also partly be ascribed to the additions of fish meal which were made to the small pond at site 1.

A further example of the possibility that spring water and the vegetation cause heterogeneity, and how this builds up during the summer, can be studied in a small bay, described by ARNEMO and NORLIN (1962, pp. 45—6). In drawing Fig. 17 a and b the values for this bay were omitted, and a special



1962: 14/6 16/7 2/8

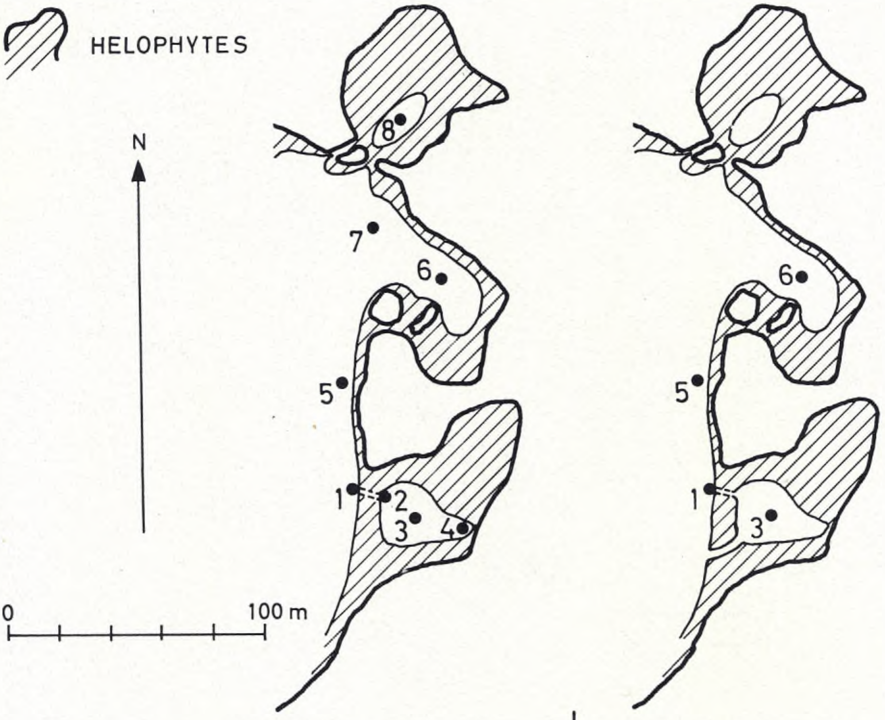
27/8 19/9

Fig. 17 b

Fig. 17 a and b. Specific conductivity at different sites in the pond, showing horizontal heterogeneity at different times.

Figure (Fig. 18) has been drawn to show the conditions there. The other two bays in the SE bay which are more or less isolated by the vegetation have been included for comparison.

It is apparent from the data in Fig. 18 that for observation points 6 and 8 no differences from the data from the SE bay can be observed, whereas observation points 2, 3 and 4 show a successive increase in specific conductivity. Spring water is probably the cause of this, even though no spring was observed here at the time when the pond was dry. ARNEMO and NORLIN suggested that the high values were caused because the post-glacial and late-glacial sand had been uncovered through the cutting away of the mull layer. This might perhaps have contributed to the increase, but the occurrence of a spring is probably the primary cause. The bottom material indirectly brings about the heterogeneity which develops, since in passing through it the spring water takes on its final ionic composition. Since the volume of water in this little bay is small, even a minor spring flow can have a large effect. The depth is about 3—4 dm. Between observation points 1 and 2 there is a dense stand of *Scirpus,* through which one can pass with a boat. How-



1961-62	1	2	3	4	5	6	7	8
4 / VIII	–	–	128	–	58	50	51	46
18 / VIII	76	117	129	158	–	–	–	–
14 / IX	114	–	139	149	76	61	–	–
8 / X	87	–	152	174	–	85	–	–
4 / XII	–	–	104	–	–	–	–	–
15 / I	–	–	398	–	–	112	–	–

1962	1	3	5	6
14 / VI	45	44	–	44
16 / VII	49	59	45	44
2 / VIII	53	57	42	43
27 / VIII	63	72	48	49
19 / IX	70	80	54	52

Fig. 18. Specific conductivity in some small bays off the SE bay at different times. The numbers in the table in the figure denote $\varkappa_{20} \cdot 10^6$ at the observation points indicated in the figure.

ever, this passage is of no importance for reciprocal exchange between the little bay and the pond just outside it. The passage has been dotted in the Figure. It is apparent from the Figure, on comparing the two years, that the external conditions changed. The dense mat of *Glyceria fluitans* and *Eleocharis palustris* which was present in 1961 was reduced in 1962 so that there was a connection between the little bay and the pond just outside it. This was a contributory cause of the influence of the spring being less pronounced in 1962 than in 1961.

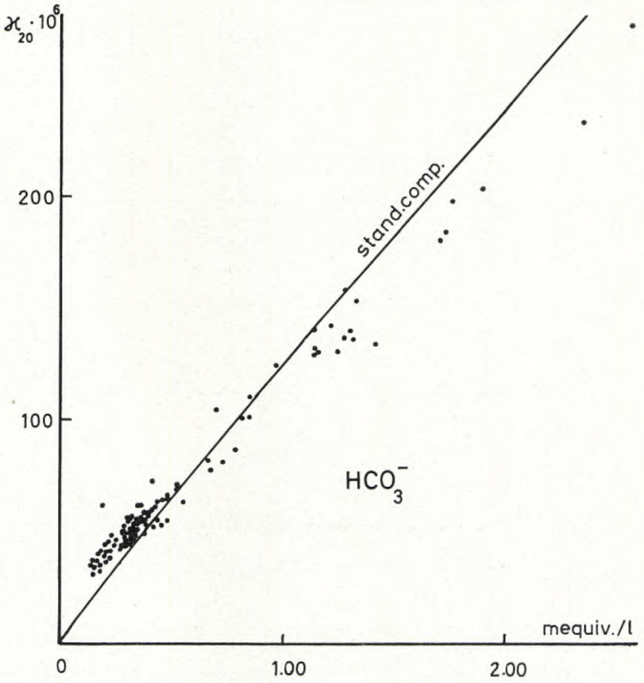


Fig. 19. Bicarbonate content in relation to "standard composition" (sensu Rodhe 1949).

7. Major constituents

(a) *Composition of the Dalälv and spring water.*

The table below shows that the ionic composition (equiv.-%) of the Dalälv water differs very much from that of the springs and how they differ from standard composition (abbreviated to stand. comp.). The mean composition of the Dalälv water during 1959—62 and of 26 spring water samples is as follows:

	Ca	Mg	Na	K	HCO_3	SO_4	Cl
Dalälv	54	26	16	4	47	44	9
Springs	84	10	5	1	87	11	2
Stand. comp.	64	17	16	3	74	16	10

(b) *Bicarbonate.*

Data on the variation in bicarbonate content are presented in Figs. 20 and 21. It is apparent from the Figures that in the summer only two sites have values higher than stand. comp. For a short time at the period of dying down of the vegetation the bicarbonate proportion changes at site 4 and U, and then exceeds stand. comp. This results from the effect of water from the springs in the SE bay. Summer 1962 was an exception, and then no analysis data gave values higher than stand. comp.

In winter, through the decrease in water volume due to ice formation, the

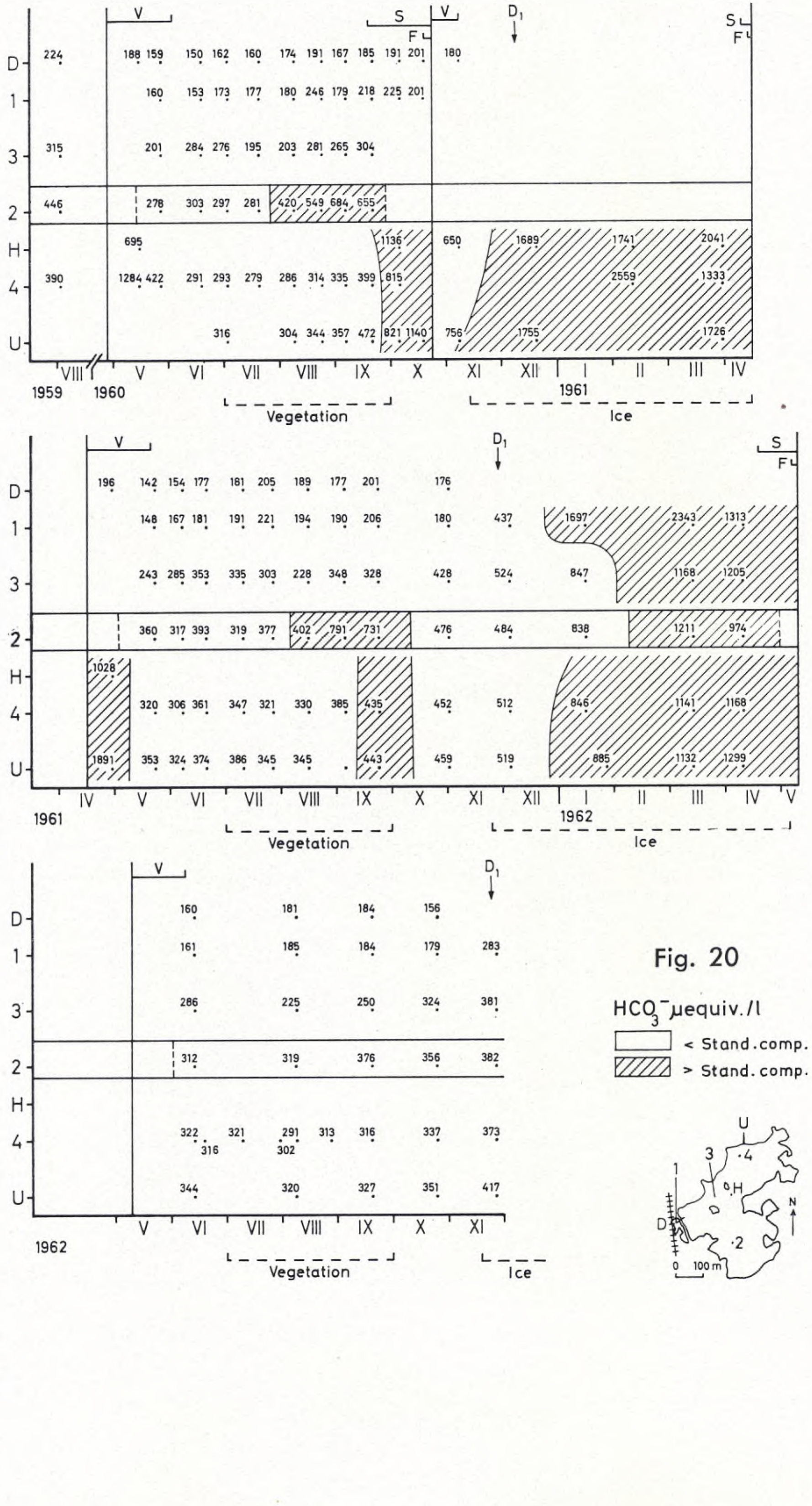

D
1
3
2
H
4
U
V
S
F
D₁
VIII
1959
1960
1961
1962
V
VI
VII
VIII
IX
X
XI
XII
I
II
III
IV
Vegetation
Ice
HCO₃⁻ µequiv./l
< Stand.comp.
> Stand. comp.
N
0
100 m

Fig. 20

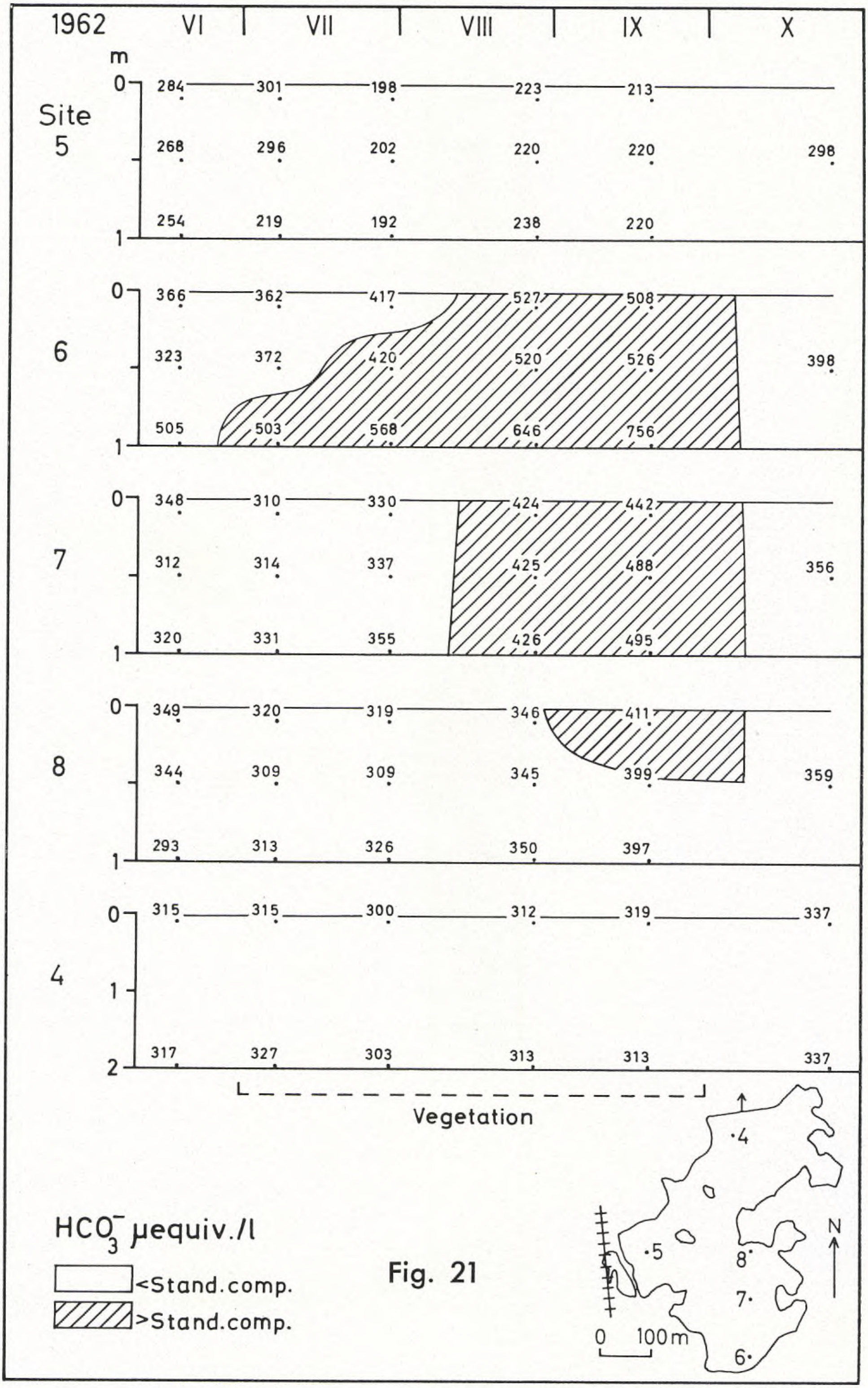

1962
VI
VII
VIII
IX
X
m
Site 5
0
284 301 198 223 213
268 296 202 220 220 298
254 219 192 238 220
1
6
0
366 362 417 527 508
323 372 420 520 526 398
505 503 568 646 756
1
7
0
348 310 330 424 442
312 314 337 425 488 356
320 331 355 426 495
1
8
0
349 320 319 346 411
344 309 309 345 399 359
293 313 326 350 397
1
4
0
315 315 300 312 319 337
1
317 327 303 313 313 337
2
Vegetation
HCO_3^- µequiv./l
<Stand.comp.
>Stand.comp.
·4
·5
8·
7·
6·
N
0
100 m

Fig. 21

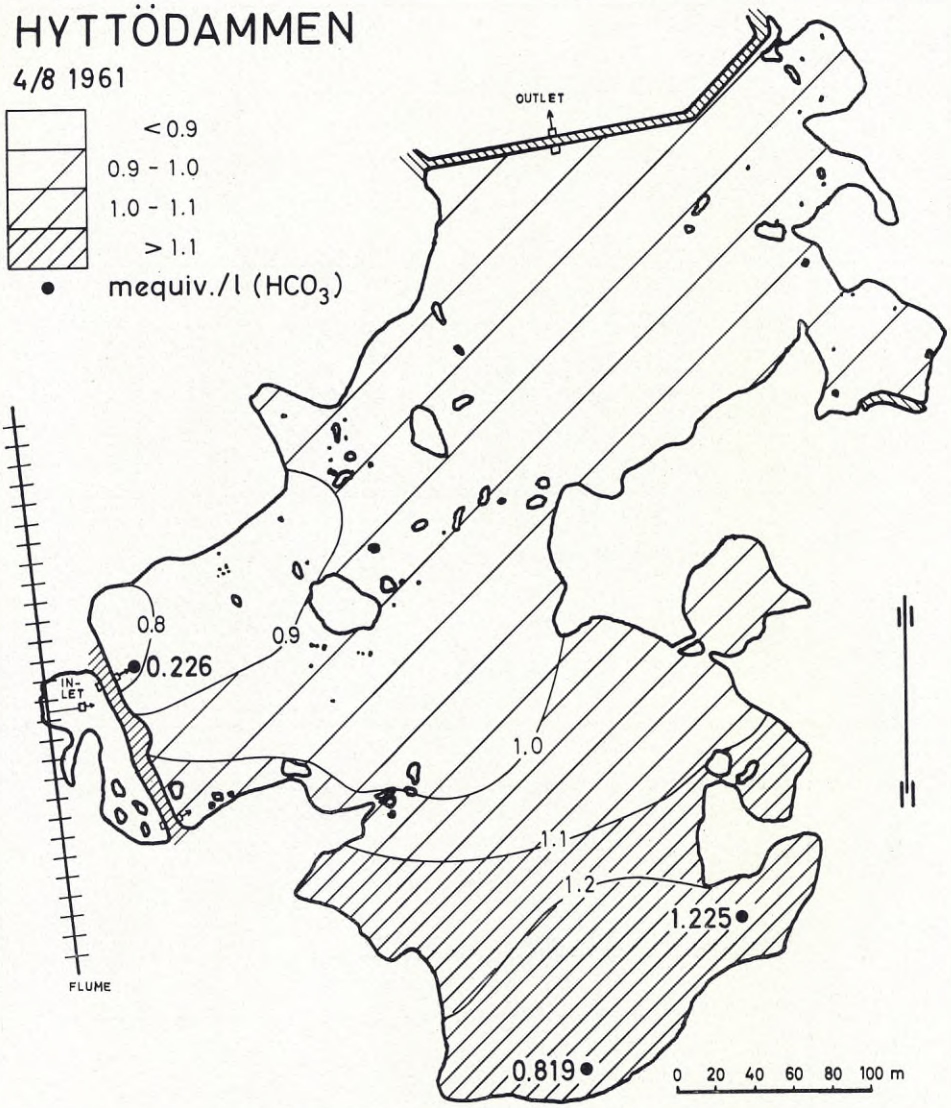


Fig. 22. Bicarbonate content at different sites in the pond, showing horizontal heterogeneity. For explanation see p. 45.

specific conductivity increases, and the bicarbonate proportion might be expected to increase to the same extent, at unchanged ionic composition. However, the composition does change, so that the proportions in the whole pond increases to values higher than stand. comp. This change goes on throughout the winter. See also Fig. 19, in which all observation data have been related to specific conductivity, and are compared with stand. comp. The observed increase probably depends mainly on the effect of the springs

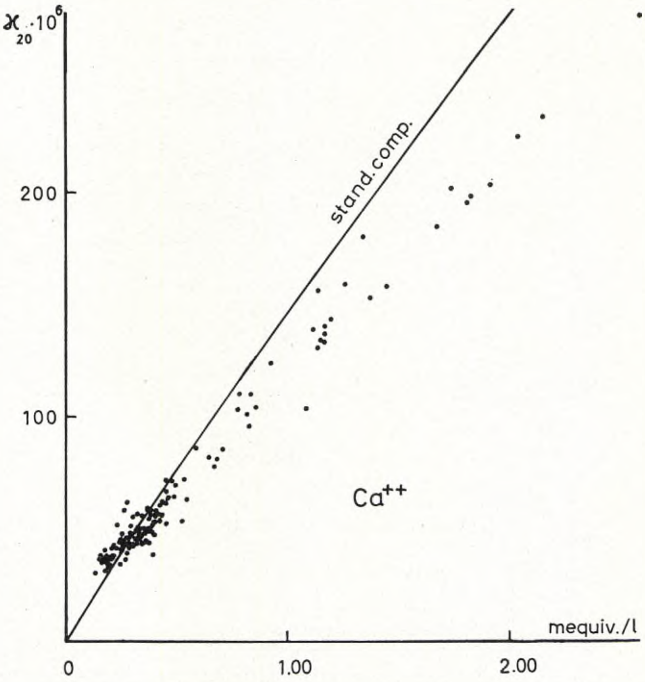


Fig. 23. Calcium content in relation to "standard composition" (sensu Rodhe 1949).

but possibly also the bottom. Breakdown processes in the uppermost layer of the sediment lead to an increase in bicarbonate content. When Dalälv water is closed off, the spring water accounts for the addition of water. Thus the proportion of bicarbonate increases (see p. 41). Increasing formation of ice reduces the volume of water (see p. 8), which in turn means that the effect of the springs on the composition is greater, though the flow may remain the same. Unfortunately there are no measurements of spring flow, so that their significance can not be calculated. It can be seen from Fig. 19 that the analysis data appear to lie on a straight line, with little scatter.

In connection with studies of the horizontal heterogeneity of the water mass and with sampling for specific conductivity measurements, samples were also taken (Aug. 4 1961) for measurements of the bicarbonate ion content. The sampling technique was the same as for specific conductivity samples. The isopletes in Fig. 22 have been drawn from the ratio between the measured bicarbonate content and the bicarbonate content given by the stand. comp. for the measured values of specific conductivity for each site. The ratios show that different parts of the pond have different proportions of bicarbonate in the ion balance. The influence of Dalälv water, with a lower proportion than the stand. comp., and of the spring water, with a higher proportion, is clear. On Aug. 4 the influence of the springs was not at its greatest (compare the situation on Aug. 4 with Sept. 11 1961, Fig. 17 a) so

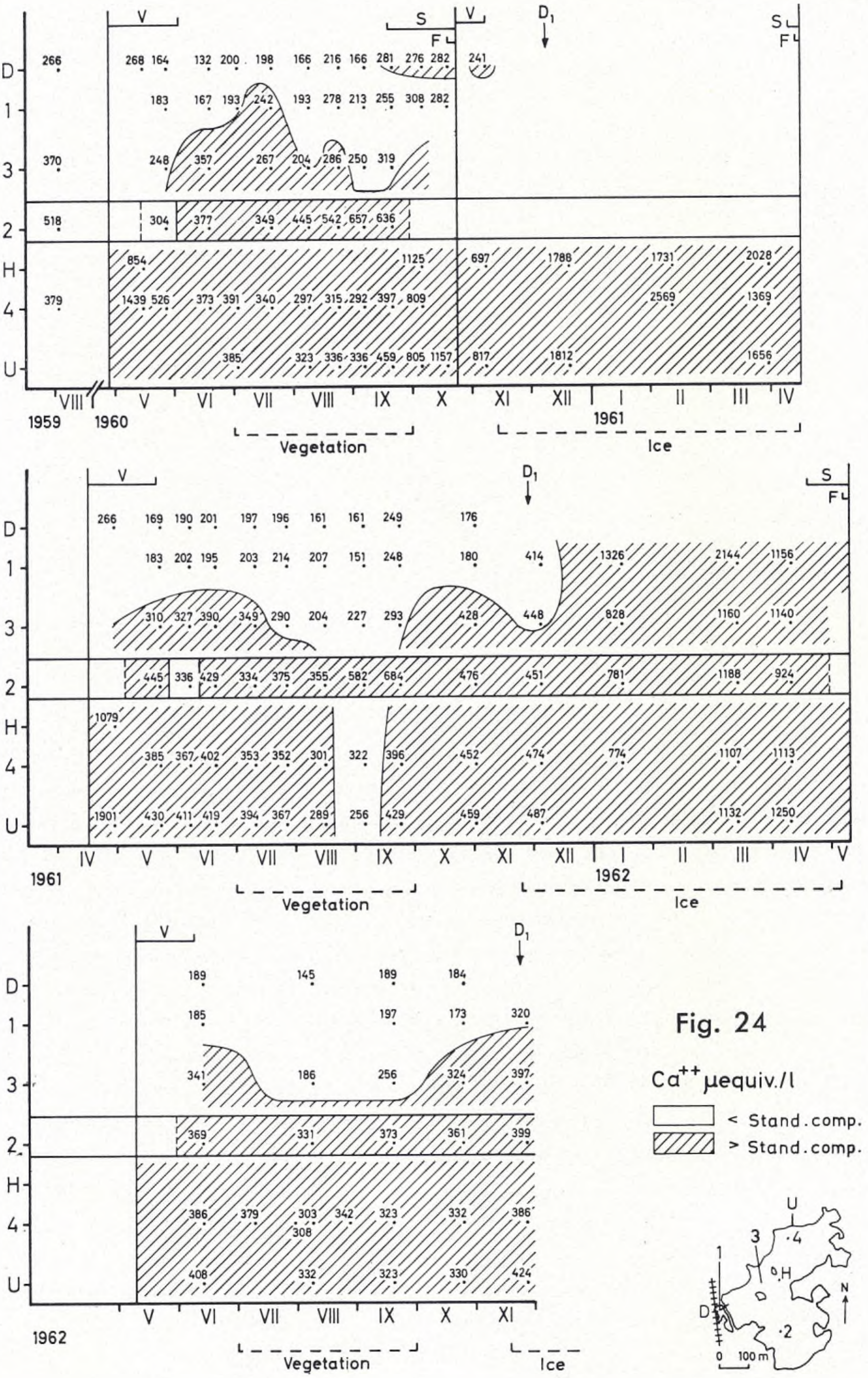


Fig. 24

Ca^{++} μequiv./l

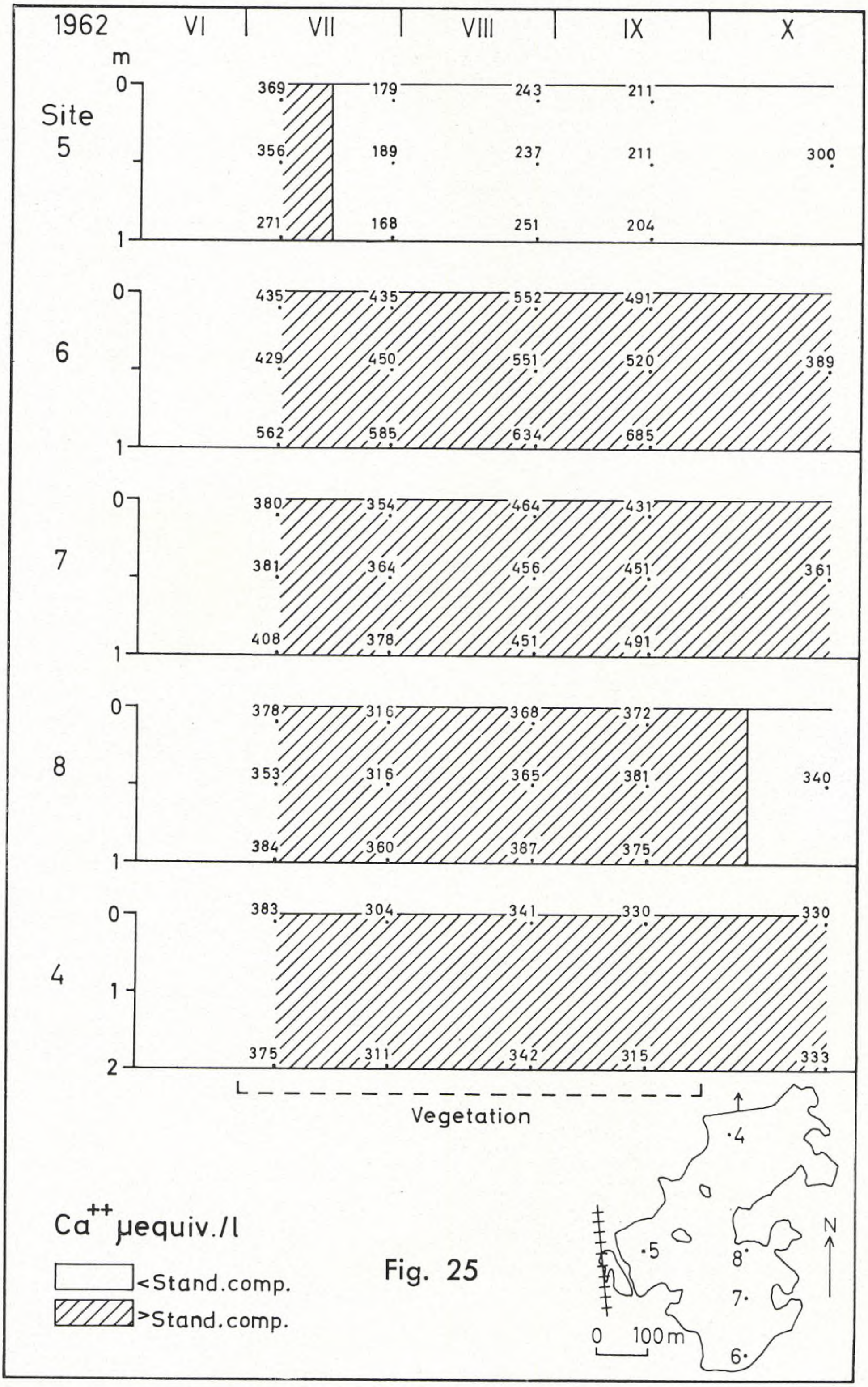

1962
VI
VII
VIII
IX
X
m
Site 5
0
1
369
356
271
179
189
168
243
237
251
211
211
204
300
6
0
1
435
429
562
435
450
585
552
551
634
491
520
685
389
7
0
1
380
381
408
354
364
378
464
456
451
431
451
491
361
8
0
1
378
353
384
316
316
360
368
365
387
372
381
375
340
4
0
1
2
383
375
304
311
341
342
330
315
330
333
Vegetation
Ca^{++} μequiv./l
☐ < Stand.comp.
▨ > Stand.comp.
·4
·5
8·
7·
6·
N
0
100 m

Fig. 25

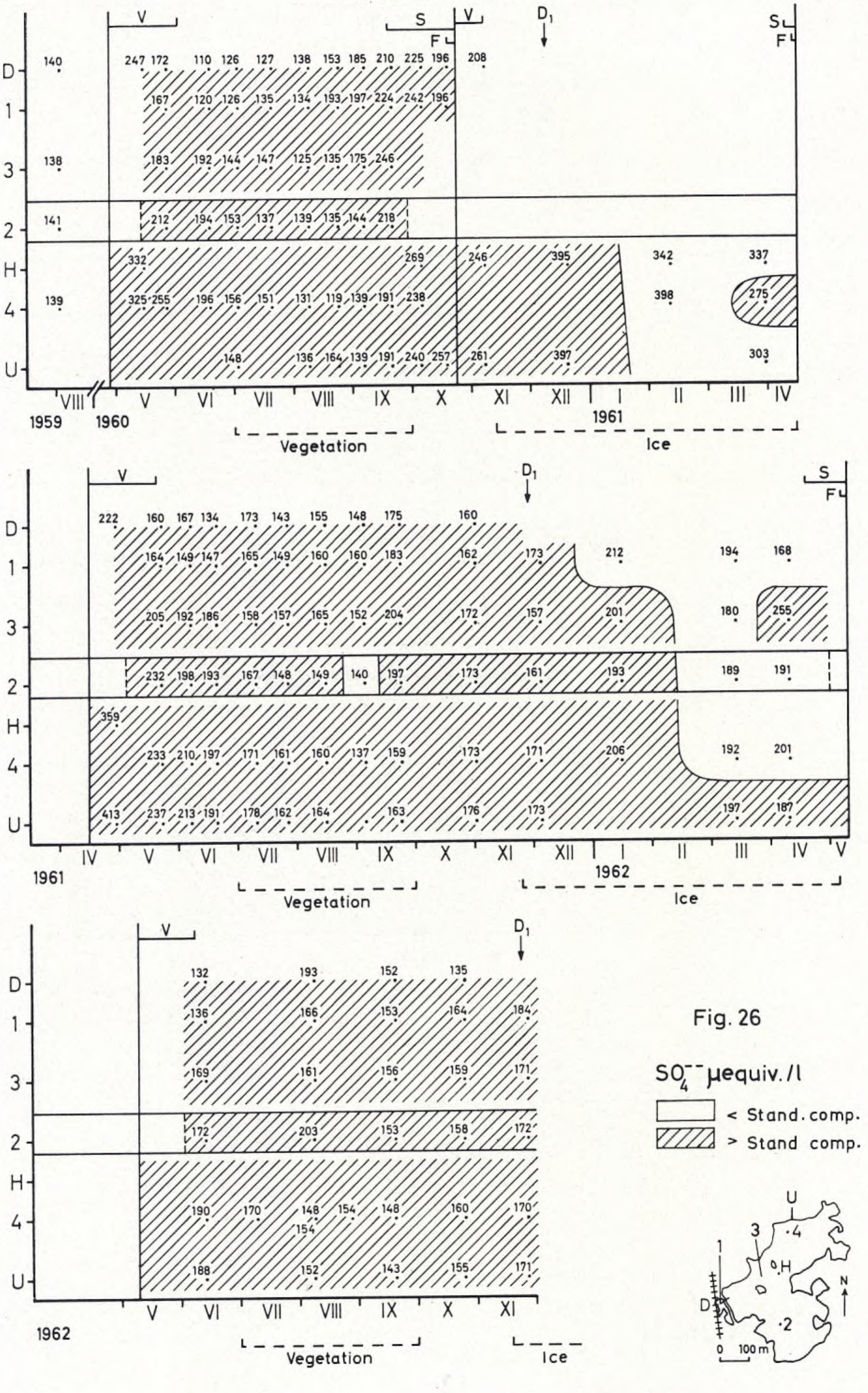

V
S
F
D1
D
1
3
2
H
4
U
140 247 172 110 126 127 138 153 185 210 225 196 208
167 120 126 135 134 193 197 224 242 196
138 183 192 144 147 125 135 175 246
141 212 194 153 137 139 135 144 218
332 269 246 395 342 337
139 325 255 196 156 151 131 119 139 191 238 398 275
148 136 164 139 191 240 257 261 397 303
VIII V VI VII VIII IX X XI XII I II III IV
1959
1960
1961
Vegetation
Ice
222 160 167 134 173 143 155 148 175 160
164 149 147 165 149 160 160 183 162 173 212 194 168
205 192 186 158 157 165 152 204 172 157 201 180 255
232 198 193 167 148 149 140 197 173 161 193 189 191
359
233 210 197 171 161 160 137 159 173 171 206 192 201
413 237 213 191 178 162 164 163 176 173 197 187
IV V VI VII VIII IX X XI XII I II III IV V
1961
1962
Vegetation
Ice
132 193 152 135
136 166 153 164 184
169 161 156 159 171
172 203 153 158 172
190 170 148 154 154 148 160 170
188 152 143 155 171
V VI VII VIII IX X XI
1962
Vegetation
Ice
SO_4^{--} μequiv./l
< Stand. comp.
> Stand comp.
U
4
3
1
H
D
2
N
0 100 m

Fig. 26

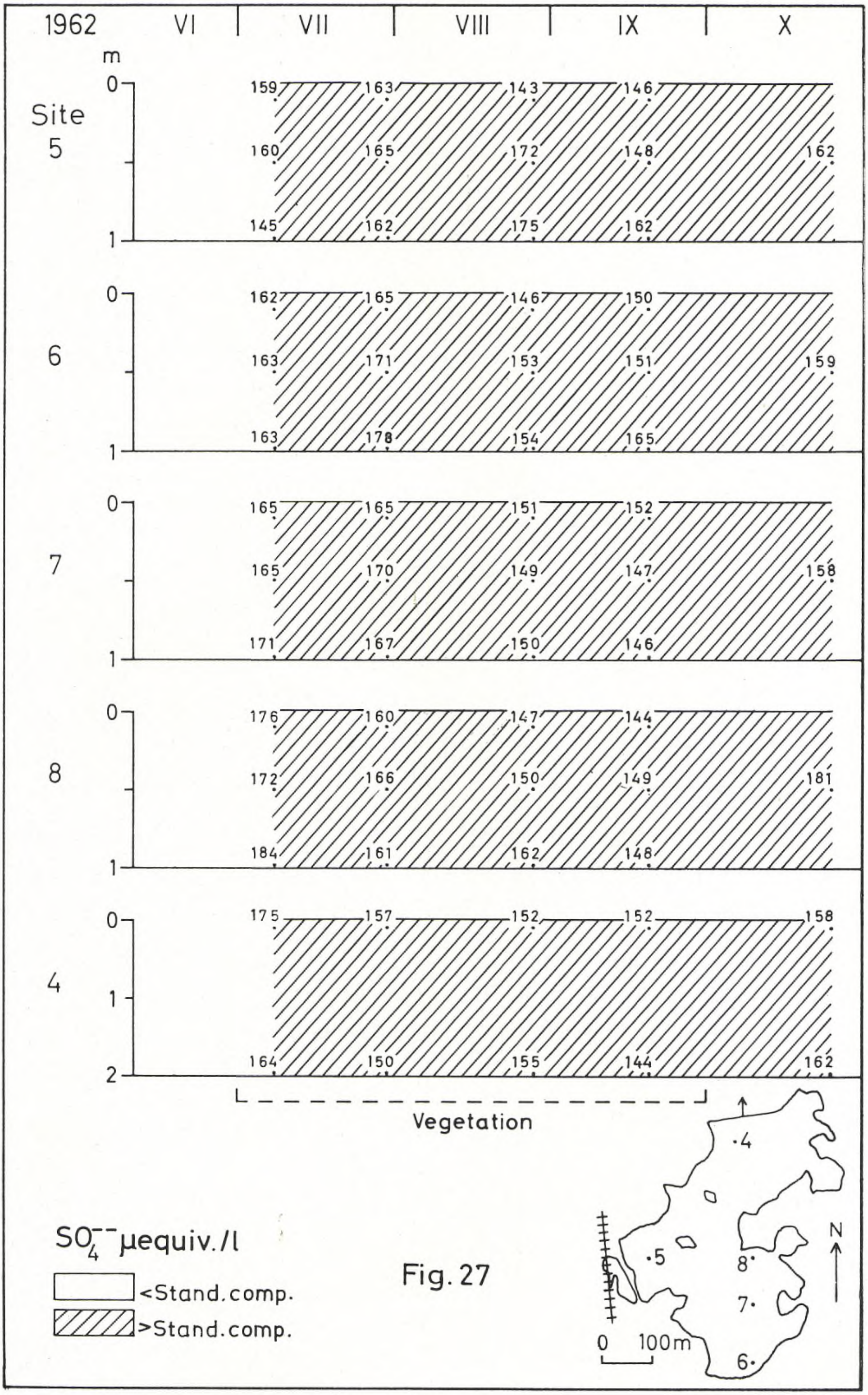

1962
VI
VII
VIII
IX
X
m
Site 5
0
1
159 163 143 146
160 165 172 148 162
145 162 175 162
6
162 165 146 150
163 171 153 151 159
163 178 154 165
7
165 165 151 152
165 170 149 147 158
171 167 150 146
8
176 160 147 144
172 166 150 149 181
184 161 162 148
4
2
175 157 152 152 158
164 150 155 144 162
Vegetation
SO_4^{--} μequiv./l
<Stand.comp.
>Stand.comp.
·4
·5
8·
7·
6·
N
0 100m

Fig. 27

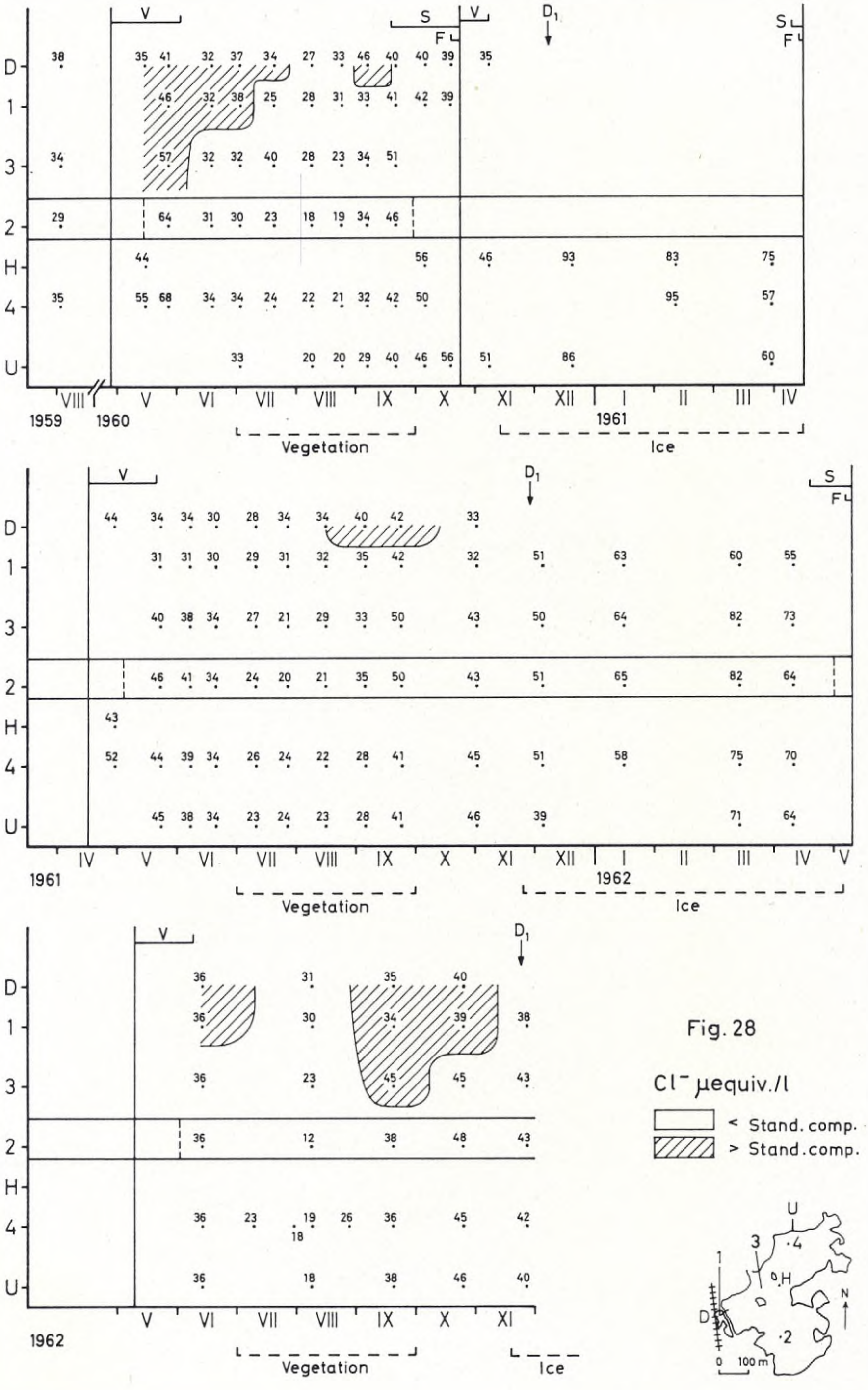

V
S
F
V
D1
S
F
D 38 35 41 32 37 34 27 33 46 40 40 39 35
1 46 32 38 25 28 31 33 41 42 39
3 34 57 32 32 40 28 23 34 51
2 29 64 31 30 23 18 19 34 46
H 44 56 46 93 83 75
4 35 55 68 34 34 24 22 21 32 42 50 95 57
U 33 20 20 29 40 46 56 51 86 60
VIII V VI VII VIII IX X XI XII I II III IV
1959 1960 1961
Vegetation
Ice
V
D1
S
F
D 44 34 34 30 28 34 34 40 42 33
1 31 31 30 29 31 32 35 42 32 51 63 60 55
3 40 38 34 27 21 29 33 50 43 50 64 82 73
2 46 41 34 24 20 21 35 50 43 51 65 82 64
H 43
4 52 44 39 34 26 24 22 28 41 45 51 58 75 70
U 45 38 34 23 24 23 28 41 46 39 71 64
IV V VI VII VIII IX X XI XII I II III IV V
1961 1962
Vegetation
Ice
V
D1
D 36 31 35 40
1 36 30 34 39 38
3 36 23 45 45 43
2 36 12 38 48 43
H
4 36 23 19 18 26 36 45 42
U 36 18 38 46 40
V VI VII VIII IX X XI
1962
Vegetation
Ice
Cl⁻ µequiv./l
< Stand. comp.
> Stand. comp.
U
3
·4
1
H
D
·2
N
0 100 m

Fig. 28

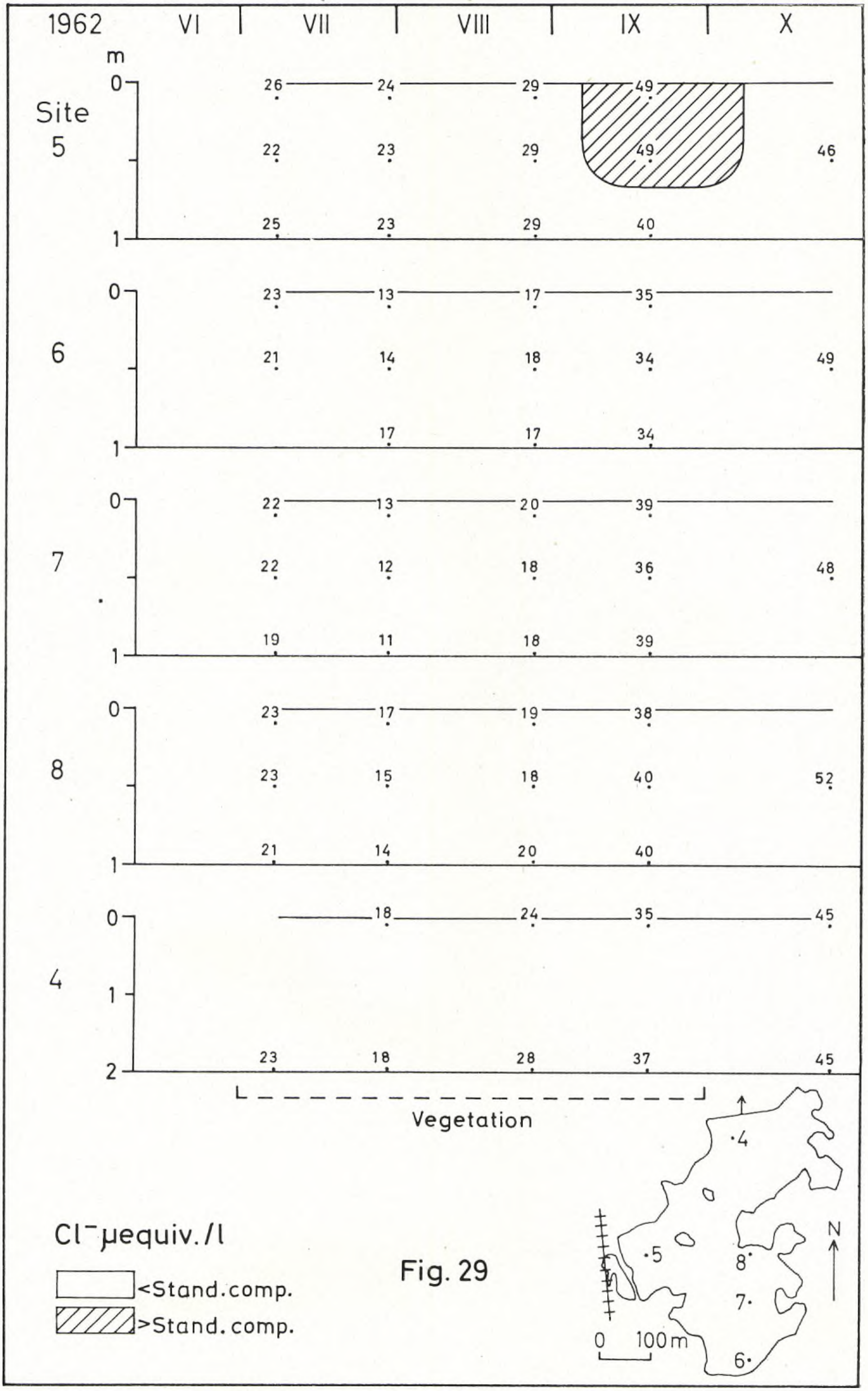

1962
VI
VII
VIII
IX
X
m
Site
5
0
1
26 24 29 49
22 23 29 49 46
25 23 29 40
6
0
1
23 13 17 35
21 14 18 34 49
17 17 34
7
0
1
22 13 20 39
22 12 18 36 48
19 11 18 39
8
0
1
23 17 19 38
23 15 18 40 52
21 14 20 40
4
0
1
2
18 24 35 45
23 18 28 37 45
Vegetation
Cl⁻ µequiv./l
<Stand. comp.
>Stand. comp.
·4
·5
8·
7·
6·
N
0 100 m

Fig. 29

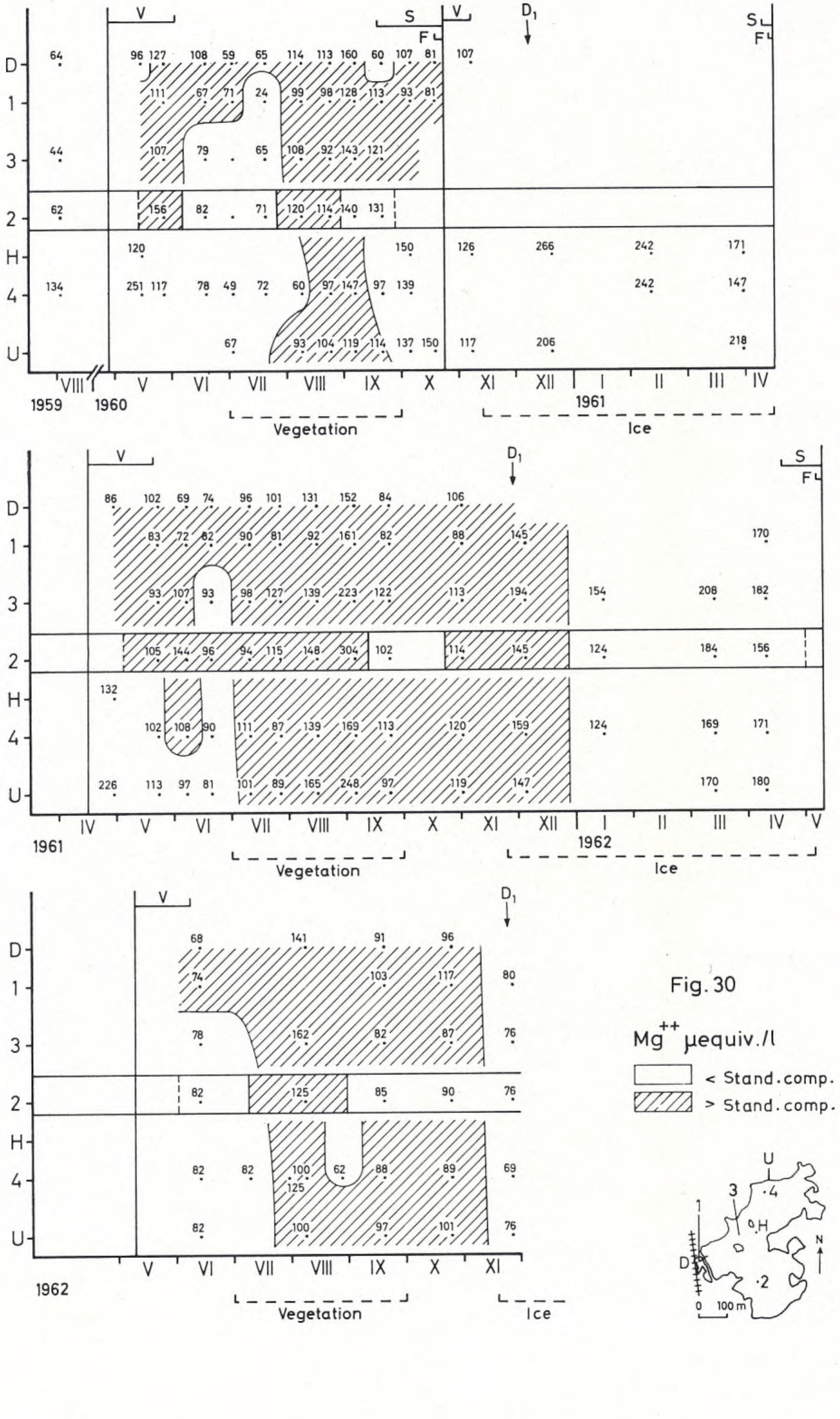

V
S
F
V
D1
S
F
D
1
3
2
H
4
U
64
96 127 108 59 65 114 113 160 60 107 81
107
111 67 71 24 99 98 128 113 93 81
44
107 79 65 108 92 143 121
62
156 82 71 120 114 140 131
120 150 126 266 242 171
134
251 117 78 49 72 60 97 147 97 139 242 147
67 93 104 119 114 137 150 117 206 218
VIII V VI VII VIII IX X XI XII I II III IV
1959 1960 1961
Vegetation
Ice
V
D1
S
F
86 102 69 74 96 101 131 152 84 106
83 72 82 90 81 92 161 82 88 145 170
93 107 93 98 127 139 223 122 113 194 154 208 182
105 144 96 94 115 148 304 102 114 145 124 184 156
132
102 108 90 111 87 139 169 113 120 159 124 169 171
226 113 97 81 101 89 165 248 97 119 147 170 180
IV V VI VII VIII IX X XI XII I II III IV V
1961 1962
Vegetation
Ice
V
D1
68 141 91 96
74 103 117 80
78 162 82 87 76
82 125 85 90 76
82 82 100 125 62 88 89 69
82 100 97 101 76
V VI VII VIII IX X XI
1962
Vegetation
Ice
Mg^{++} µequiv./l
< Stand.comp.
> Stand.comp.
U
3
4
1
H
N
D
2
0 100 m

Fig. 30

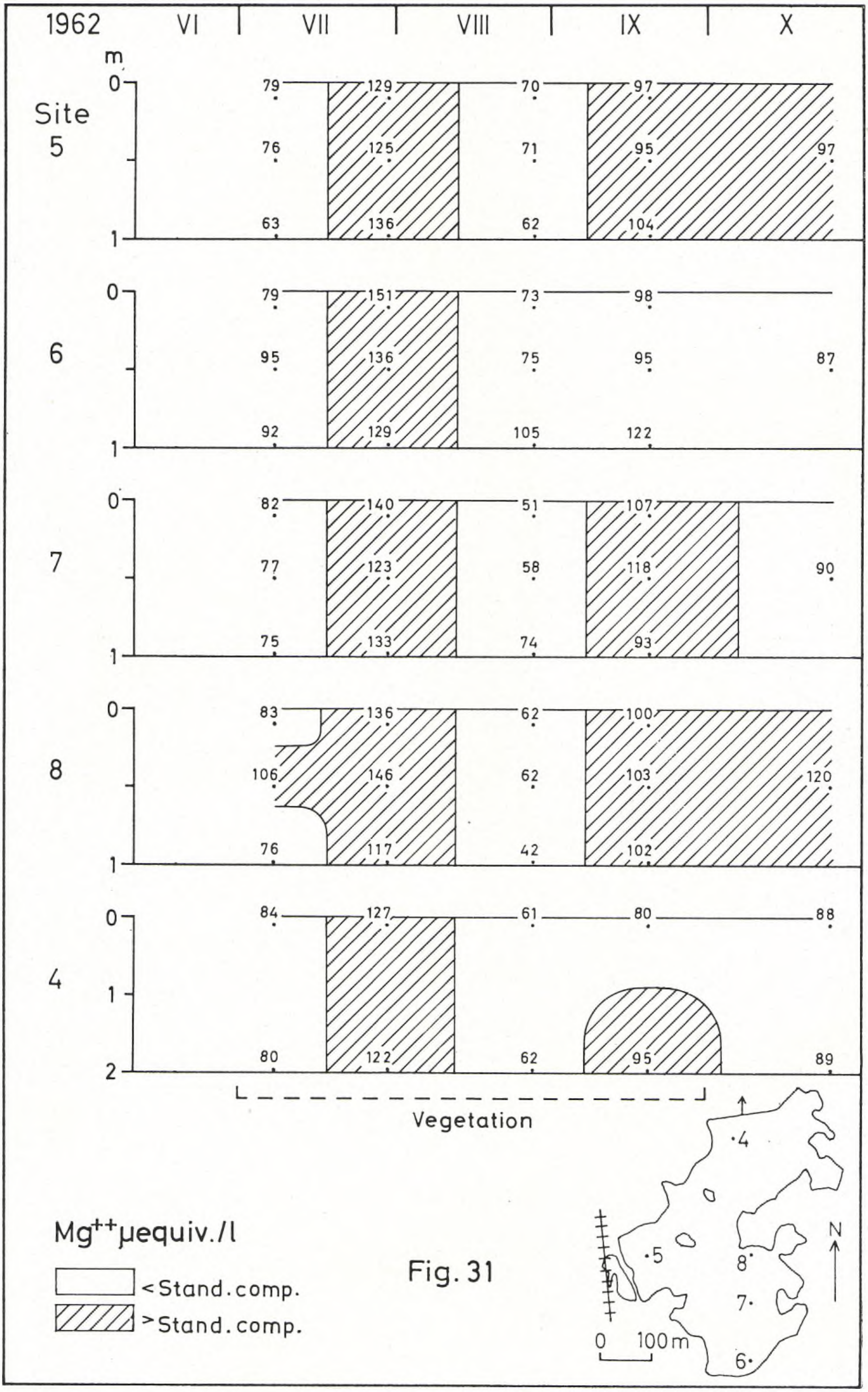

1962
VI
VII
VIII
IX
X
m
Site 5
Site 6
Site 7
Site 8
Site 4
0
1
2
79 129 70 97
76 125 71 95 97
63 136 62 104
79 151 73 98
95 136 75 95 87
92 129 105 122
82 140 51 107
77 123 58 118 90
75 133 74 93
83 136 62 100
106 146 62 103 120
76 117 42 102
84 127 61 80 88
80 122 62 95 89
Vegetation
Mg++ µequiv./l
< Stand. comp.
> Stand. comp.
·4
·5
8·
7·
6·
N
0 100 m

Fig. 31

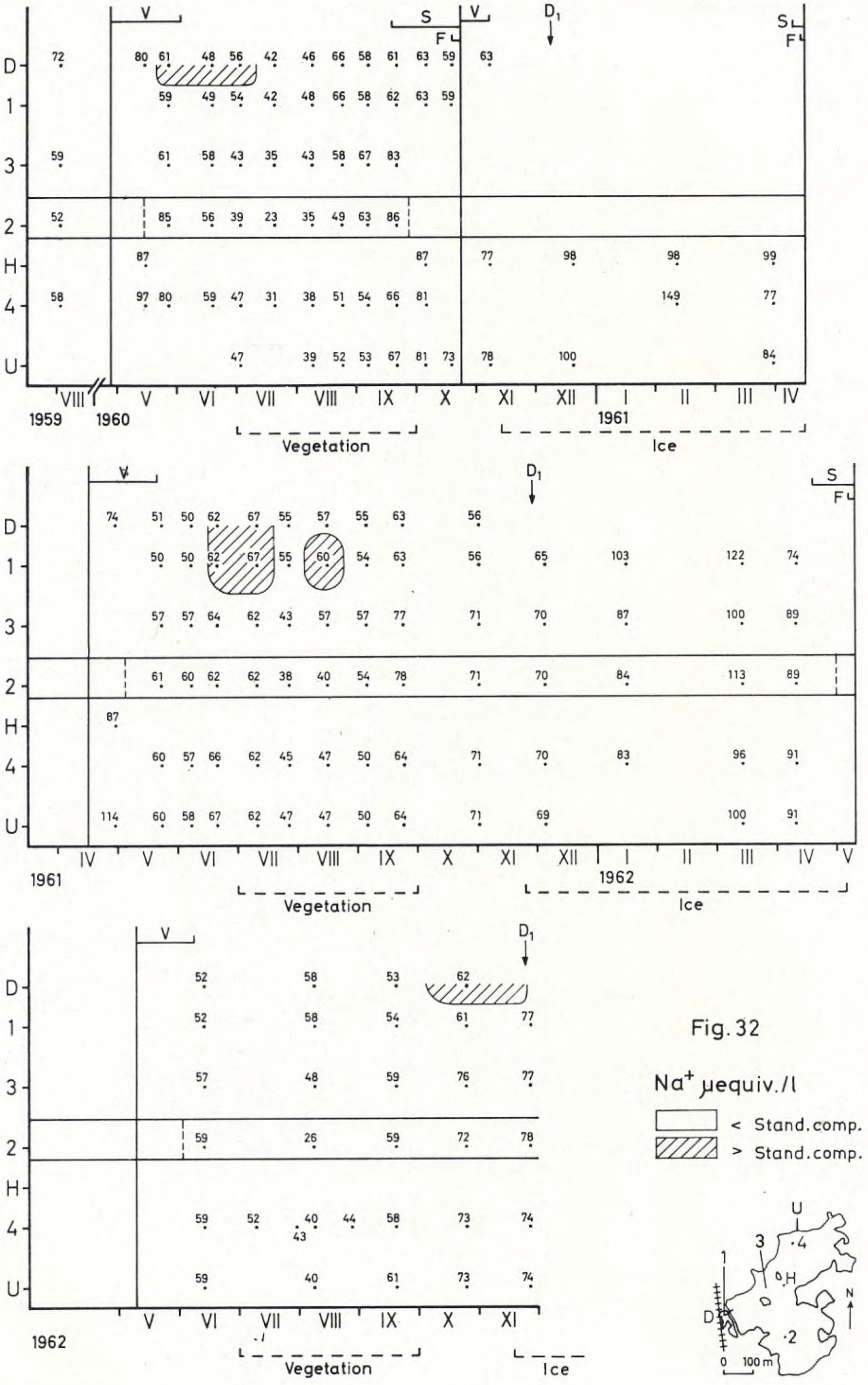

V
S
F
V
D1
S
F
D
1
3
2
H
4
U
72 80 61 48 56 42 46 66 58 61 63 59 63
59 49 54 42 48 66 58 62 63 59
59 61 58 43 35 43 58 67 83
52 85 56 39 23 35 49 63 86
87 87 77 98 98 99
58 97 80 59 47 31 38 51 54 66 81 149 77
47 39 52 53 67 81 73 78 100 84
VIII V VI VII VIII IX X XI XII I II III IV
1959 1960 1961
Vegetation
Ice
V
D1
S
F
74 51 50 62 67 55 57 55 63 56
50 50 62 67 55 60 54 63 56 65 103 122 74
57 57 64 62 43 57 57 77 71 70 87 100 89
61 60 62 62 38 40 54 78 71 70 84 113 89
87
60 57 66 62 45 47 50 64 71 70 83 96 91
114 60 58 67 62 47 47 50 64 71 69 100 91
IV V VI VII VIII IX X XI XII I II III IV V
1961 1962
Vegetation
Ice
V
D1
52 58 53 62
52 58 54 61 77
57 48 59 76 77
59 26 59 72 78
59 52 40 43 44 58 73 74
59 40 61 73 74
V VI VII VIII IX X XI
1962
Vegetation
Ice
Na+ µequiv./l
< Stand.comp.
> Stand.comp.
U
3
4
1
H
D
2
N
0 100 m

Fig. 32

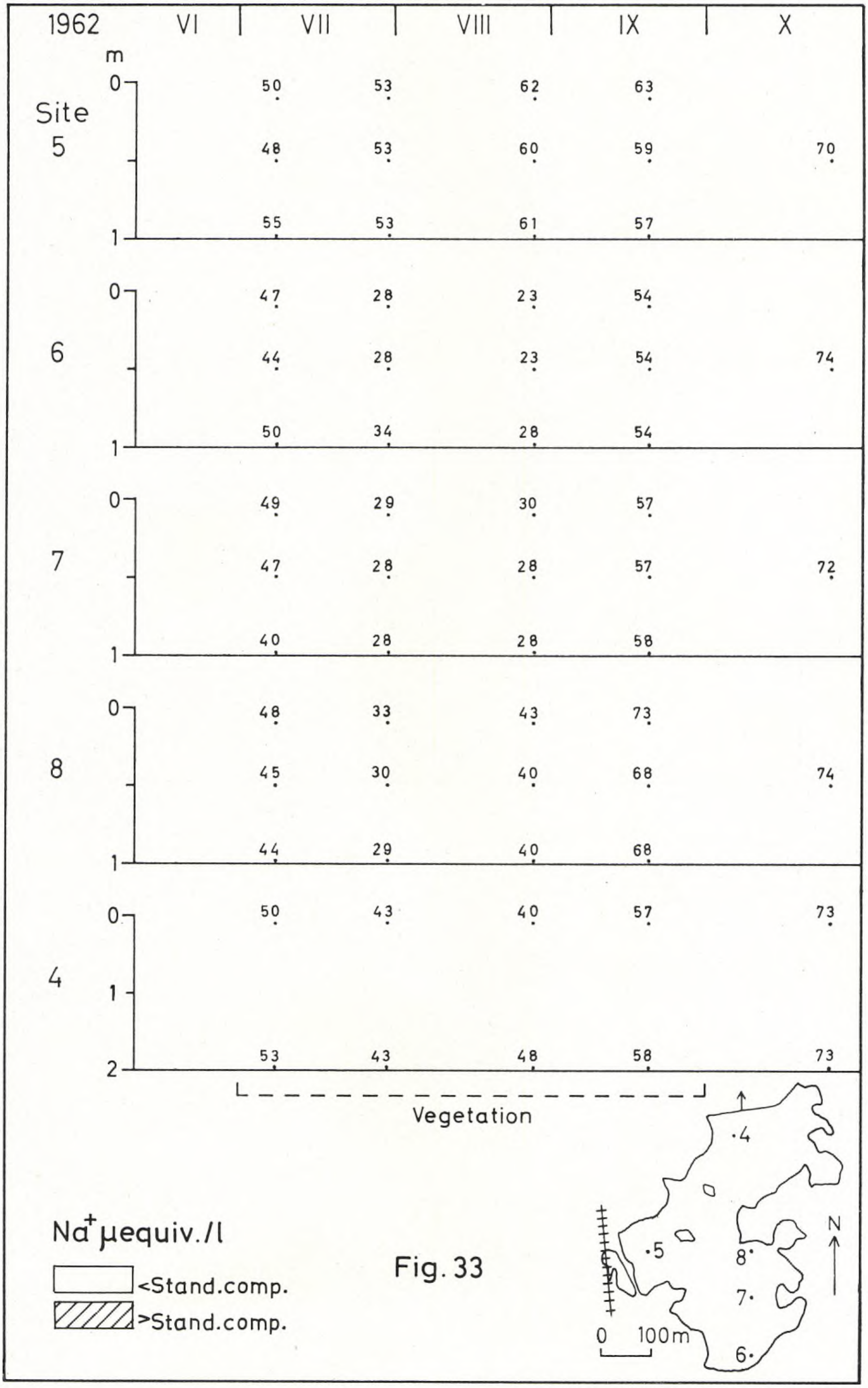

1962
VI
VII
VIII
IX
X
m
Site
5
0
50 53 62 63
48 53 60 59 70
55 53 61 57
1
6
0
47 28 23 54
44 28 23 54 74
50 34 28 54
1
7
0
49 29 30 57
47 28 28 57 72
40 28 28 58
1
8
0
48 33 43 73
45 30 40 68 74
44 29 40 68
1
4
0
50 43 40 57 73
1
53 43 48 58 73
2
Vegetation
Na⁺ µequiv./l
<Stand.comp.
>Stand.comp.
·4
·5
8·
7·
6·
N
0 100m

Fig. 33

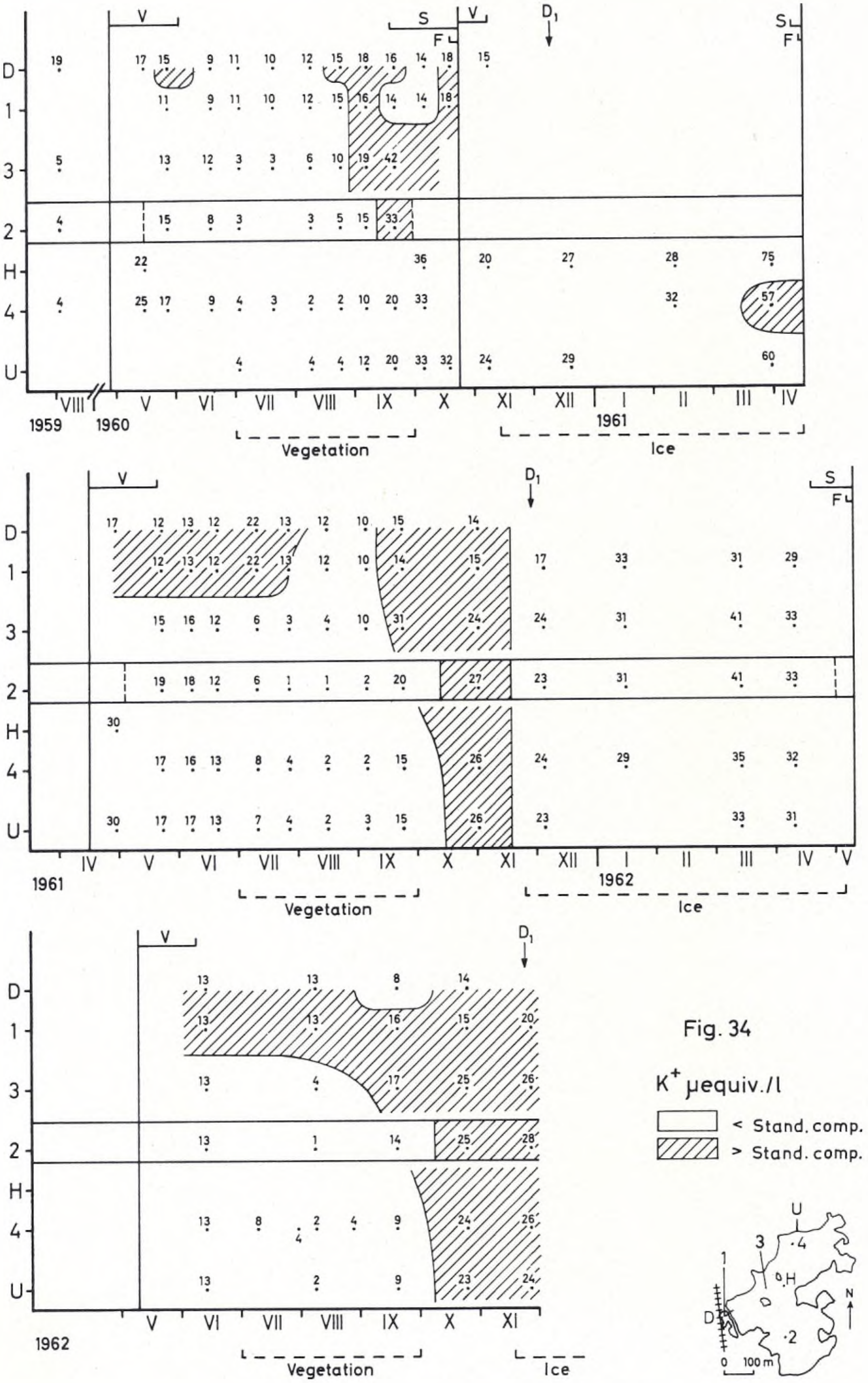

V
S
F
D₁
D
1
3
2
H
4
U
VIII
V
VI
VII
VIII
IX
X
XI
XII
I
II
III
IV
1959
1960
1961
1962
Vegetation
Ice
K⁺ µequiv./l
< Stand. comp.
> Stand. comp.
0 100 m
N

Fig. 34

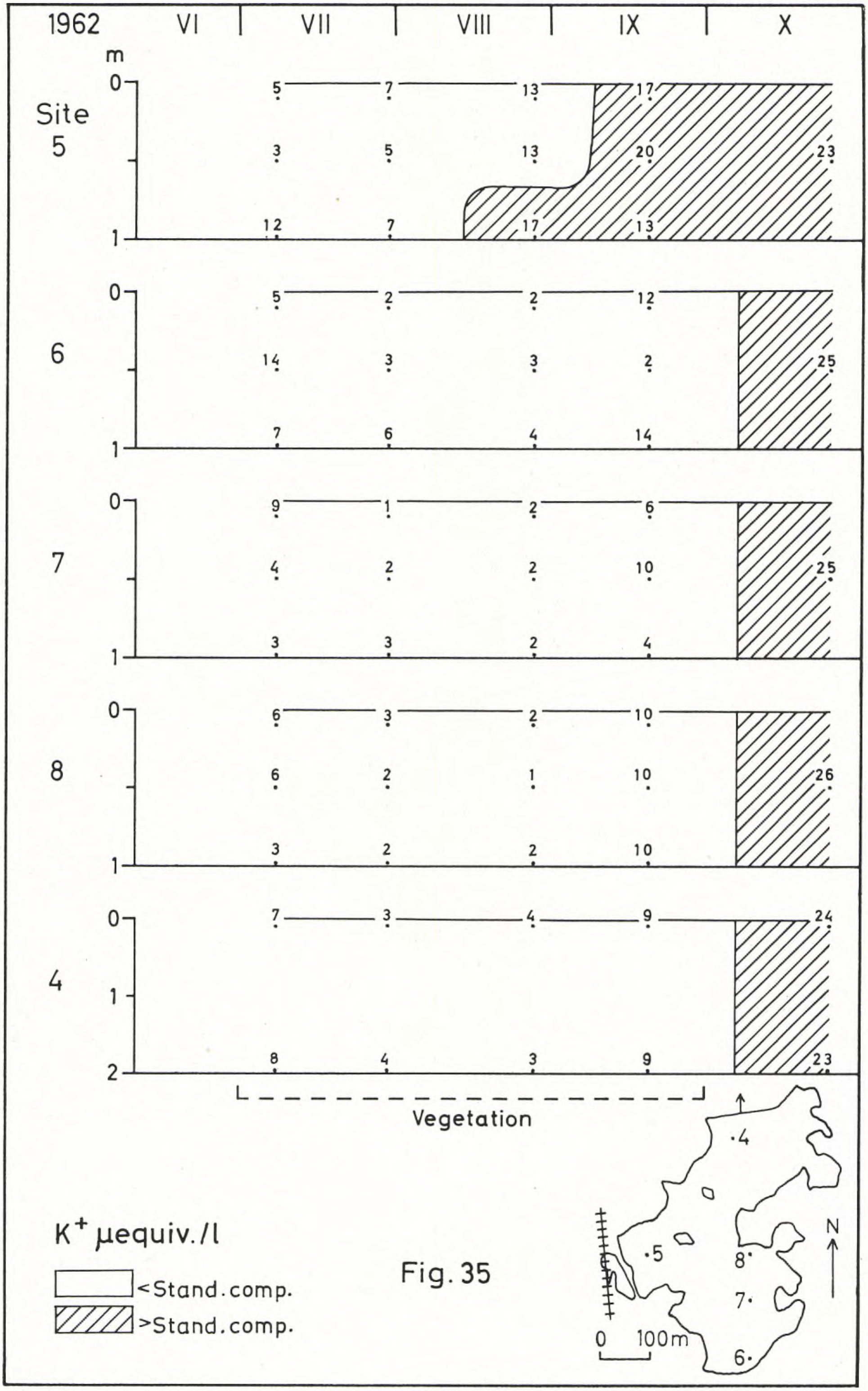

1962
VI
VII
VIII
IX
X
m
Site 5
0
1
5 7 13 17
3 5 13 20 23
12 7 17 13
6
0
1
5 2 2 12
14 3 3 2 25
7 6 4 14
7
0
1
9 1 2 6
4 2 2 10 25
3 3 2 4
8
0
1
6 3 2 10
6 2 1 10 26
3 2 2 10
4
0
1
2
7 3 4 9 24
8 4 3 9 23
Vegetation
K⁺ µequiv./l
<Stand.comp.
>Stand.comp.
·4
·5
8·
7·
6·
N
0 100m

Fig. 35

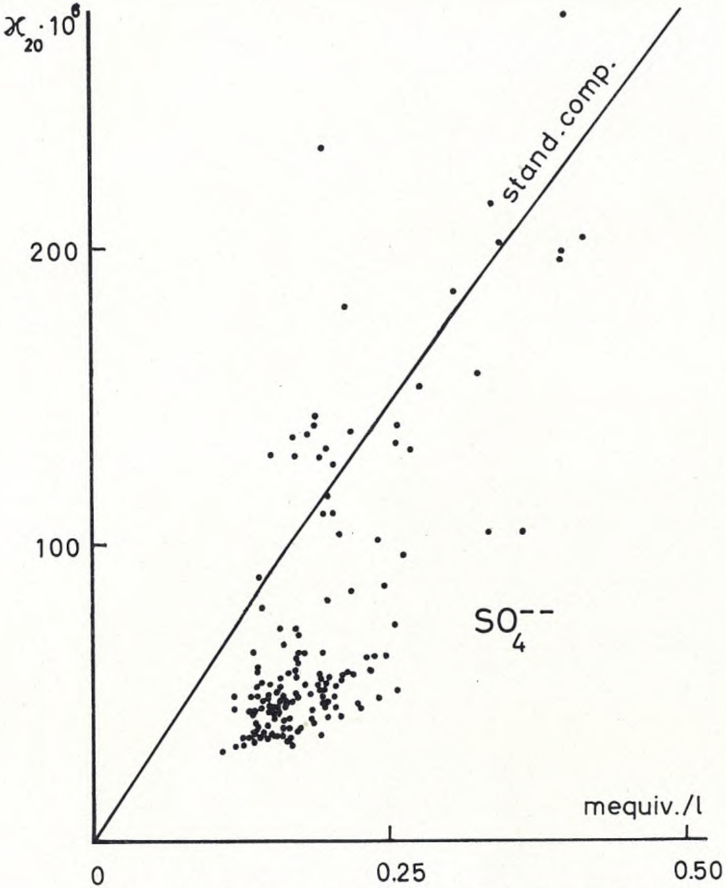


Fig. 36. Sulphate content in relation ot "standard composition" (sensu Rodhe 1949).

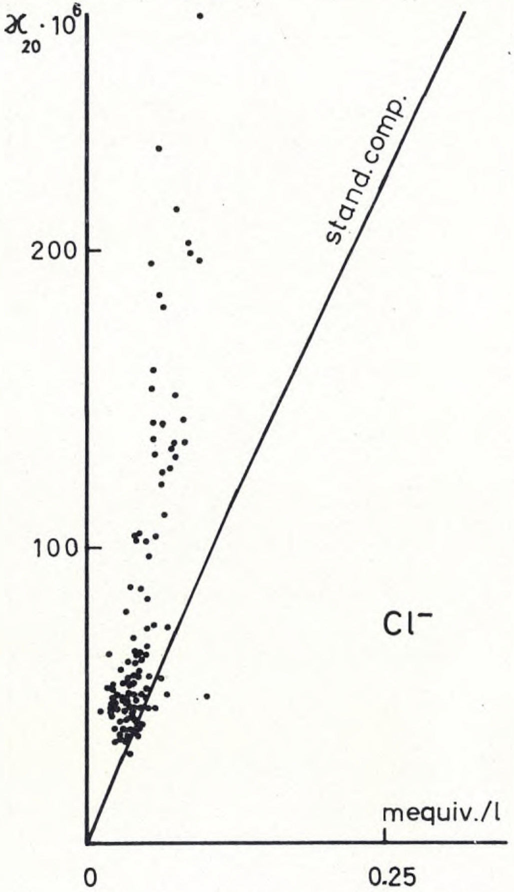


Fig. 37. Chloride content in relation to "standard composition" (sensu Rodhe (1949).

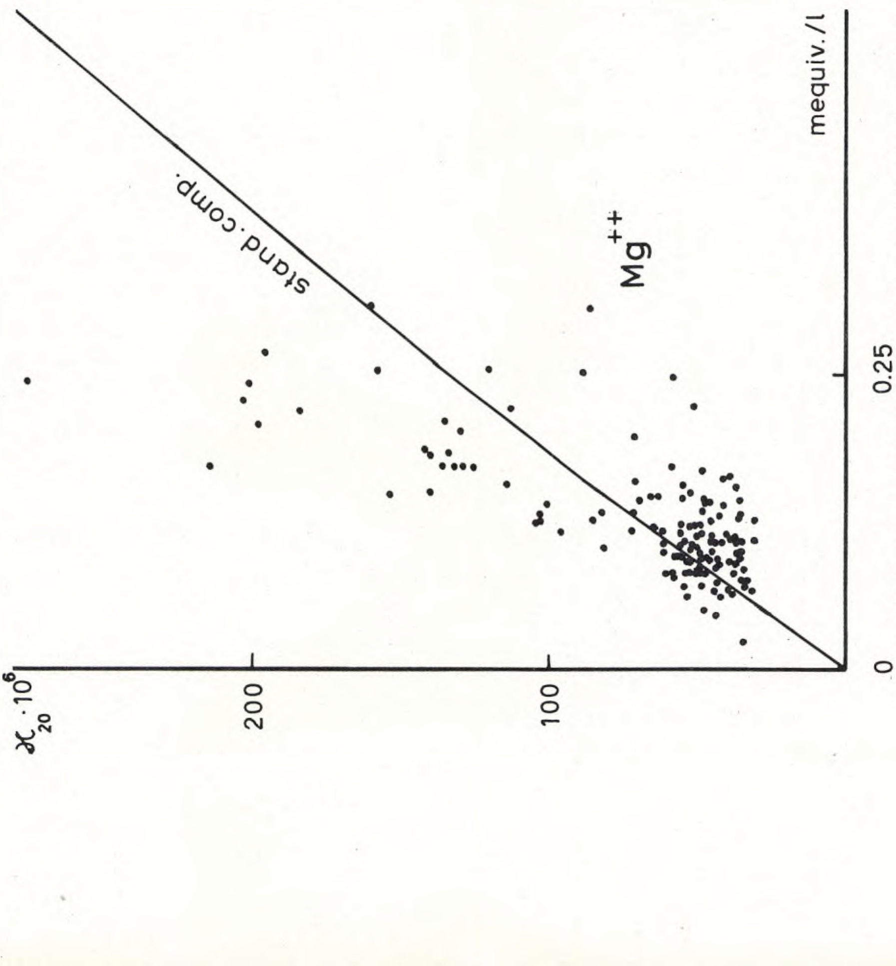


Fig. 38. Magnesium content in relation to "standard composition" (sensu Rodhe 1949).

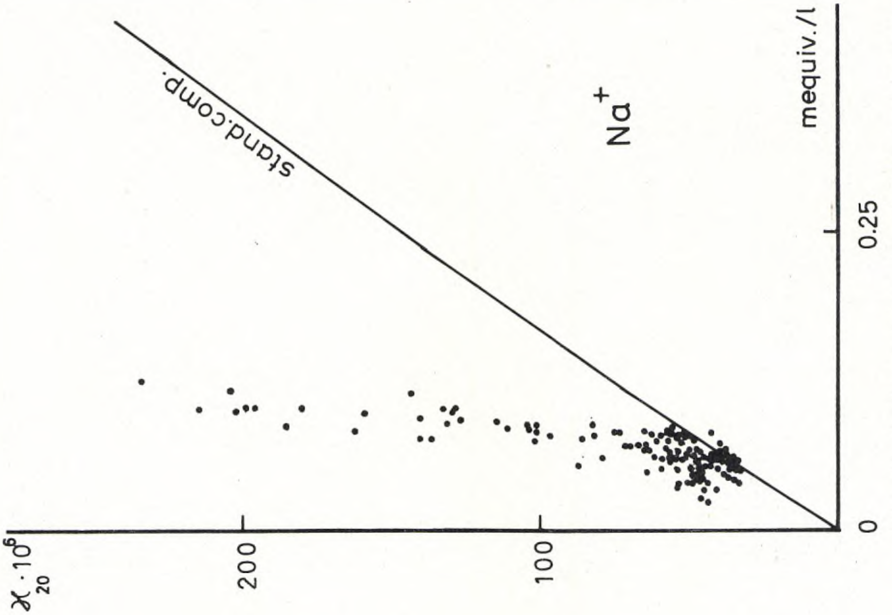


Fig. 39. Sodium content in relation to "Standard composition" (sensu Rodhe 1949).

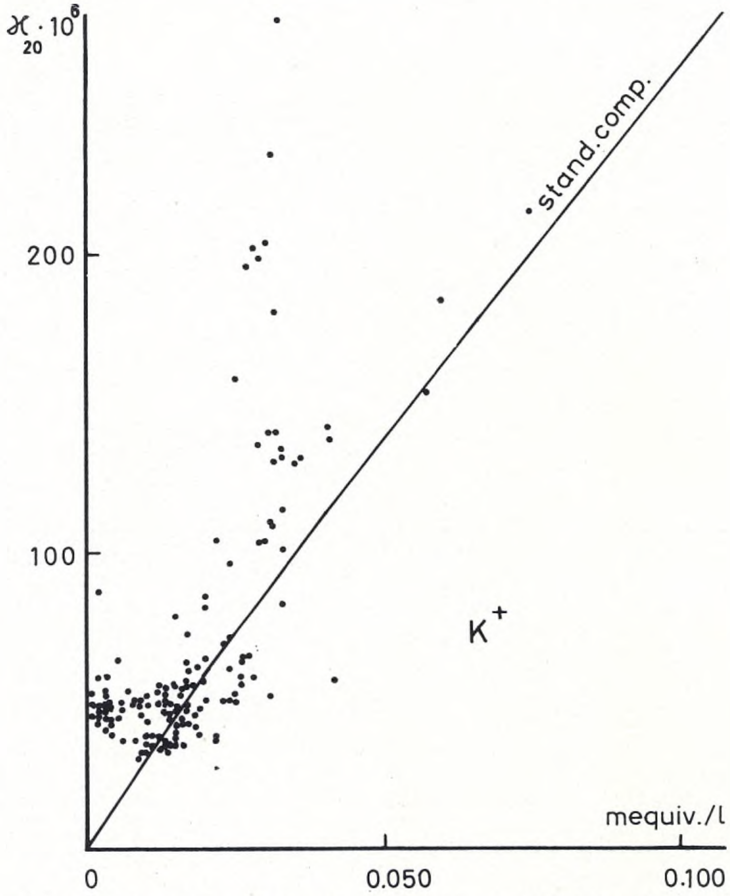


Fig. 40. Potassium content in relation to "standard composition" (sensu Rodhe 1949).

that the differences between the different parts of the pond would be expected to be even more striking immediately before the horizontal mixing in connection with the dying down of the vegetation. The vegetation is fairly uniformly distributed in the Dalälv side and the SE bay. Its effect on bicarbonate content through assimilation may be assumed to be similar in these areas.

(c) *Calcium.*

As shown by Figs. 24 and 25, the calcium proportion is lower than stand. comp. in Dalälv water and those parts of the pond which are influenced by this water, and higher than stand. comp. in the SE bay. At sites 4 and U there are also higher proportions than stand. comp., as a result of mixing of the masses of water. In Fig. 23 the analysis data have been plotted in relation to specific conductivity and they show a good agreement. The increase in proportion of bicarbonate ions over the expected during the winter is seen to have its equivalent in content of calcium ions. This increase is also attributed partly to the sediment processes but mainly to spring water.

(d) *Sulphate, chloride, magnesium, sodium and potassium.*

In summary, it may be said for these ions that their proportions decrease during the winter and almost all, sooner or later, are lower than stand. comp. See Figs. 26—35. These changes are probably attributable to the influence of spring water, which has lower proportions than stand. comp. During summer and autumn proportions of sulphate and magnesium higher than stand. comp. can be observed, while those of sodium, potassium and chloride are usually less. It is virtually always for Dalälv water and site 1 that proportions of the last three are higher than stand. comp. During the summer the absolute contents of sodium, potassium and chloride decrease rapidly and then increase, as is discussed on pp. 85), where the change in potassium proportion to a value higher than stand. comp. is also explained.

In Figs. 36—40 the amount of the various ions is related to the stand. comp. for corresponding values of specific conductivity. Sodium and chloride values appear to lie on a straight line, with little scatter, while the others are more scattered.

8. Minor constituents

(a) *Phosphorus.*

Data on contents of phosphate-P are shown in Figs. 41 and 42; on total-P contents in Figs. 43 and 44; and the proportion of phosphate-P in the total, as calculated from these, in Figs. 45 and 46.

The phosphate-P is higher in the summer in the SE bay than in the other parts of the pond. The observed values are sometimes so high that an effect from pollution might be suspected. However, Hyttödammen is not polluted, and so the high values must be due to other causes (see pp. 89—90). The phosphorus content increases in the winter.

Total-P content is least in Dalälv water and at site 1 in the summer. The contents in the SE bay are sometimes higher than at other parts of the pond. In winter the contents increase.

Phosphate-P as a percentage of total-P is higher in the SE bay than at other parts of the pond. At site 8, the proportion is especially high, with *c.* 50 % during August and September.

The spring water varied between 0.3—27 with a mean content of 5.4 μg phosphate-P per litre and 4.1—60 with a mean content of 15.3 μg total-P per litre. The relation between their means is 0.36.

To judge from the measured values it seems that phosphorus is not a limiting substance for production in Hyttödammen.

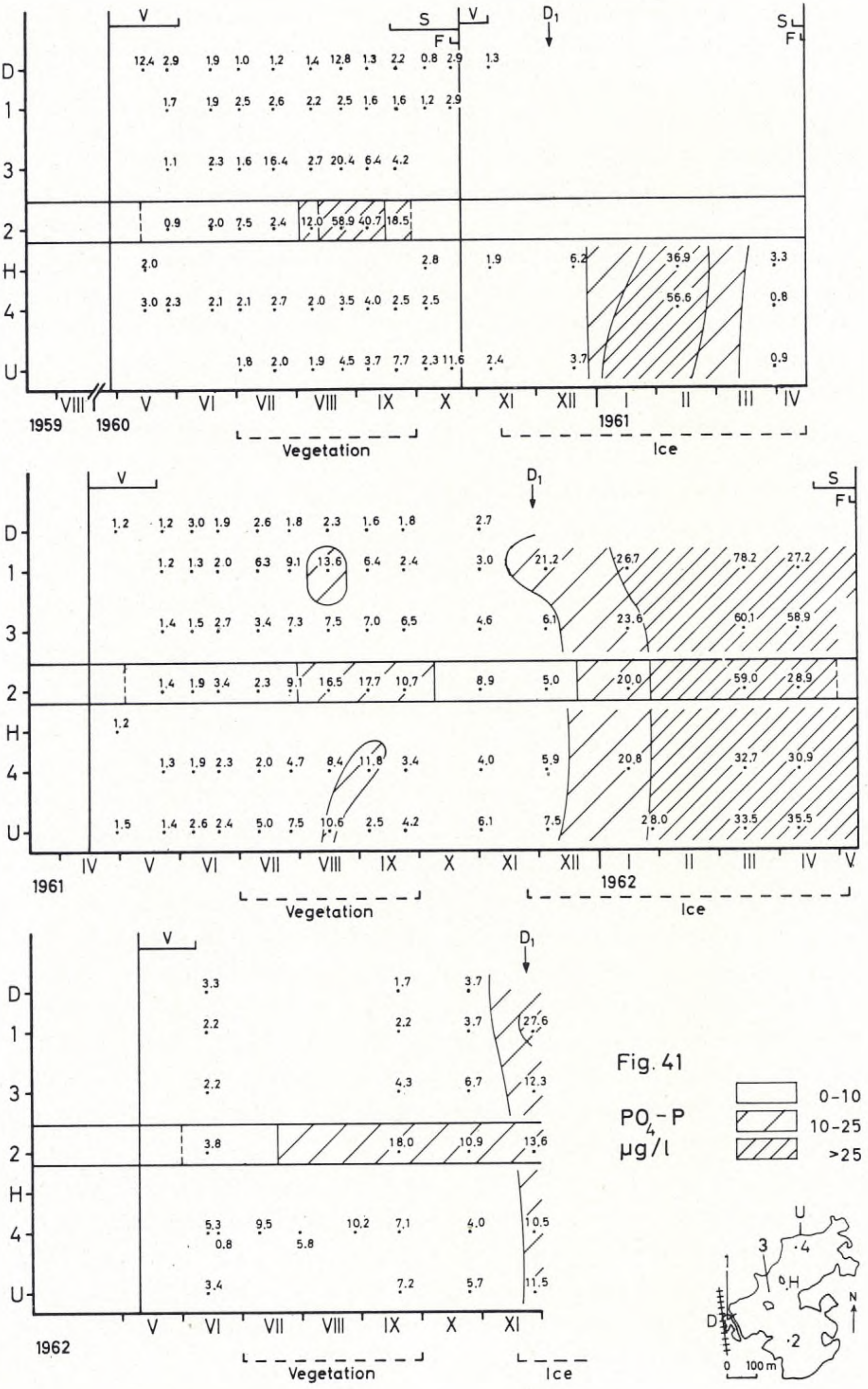

D
1
3
2
H
4
U
V
S
F
D1
12.4 2.9 1.9 1.0 1.2 1.4 12.8 1.3 2.2 0.8 2.9 1.3
1.7 1.9 2.5 2.6 2.2 2.5 1.6 1.6 1.2 2.9
1.1 2.3 1.6 16.4 2.7 20.4 6.4 4.2
0.9 2.0 7.5 2.4 12.0 58.9 40.7 18.5
2.0 2.8 1.9 6.2 36.9 3.3
3.0 2.3 2.1 2.1 2.7 2.0 3.5 4.0 2.5 2.5 56.6 0.8
1.8 2.0 1.9 4.5 3.7 7.7 2.3 11.6 2.4 3.7 0.9
VIII V VI VII VIII IX X XI XII I II III IV
1959 1960 1961
Vegetation
Ice
1.2 1.2 3.0 1.9 2.6 1.8 2.3 1.6 1.8 2.7
1.2 1.3 2.0 6.3 9.1 13.6 6.4 2.4 3.0 21.2 26.7 78.2 27.2
1.4 1.5 2.7 3.4 7.3 7.5 7.0 6.5 4.6 6.1 23.6 60.1 58.9
1.4 1.9 3.4 2.3 9.1 16.5 17.7 10.7 8.9 5.0 20.0 59.0 28.9
1.2
1.3 1.9 2.3 2.0 4.7 8.4 11.8 3.4 4.0 5.9 20.8 32.7 30.9
1.5 1.4 2.6 2.4 5.0 7.5 10.6 2.5 4.2 6.1 7.5 28.0 33.5 35.5
IV V VI VII VIII IX X XI XII I II III IV V
1961 1962
Vegetation
Ice
3.3 1.7 3.7
2.2 2.2 3.7 27.6
2.2 4.3 6.7 12.3
3.8 18.0 10.9 13.6
5.3 9.5 10.2 7.1 4.0 10.5
0.8 5.8
3.4 7.2 5.7 11.5
V VI VII VIII IX X XI
1962
Vegetation
Ice
PO4-P
µg/l
0-10
10-25
>25
U
3
1
4
H
D
2
N
0 100 m

Fig. 41

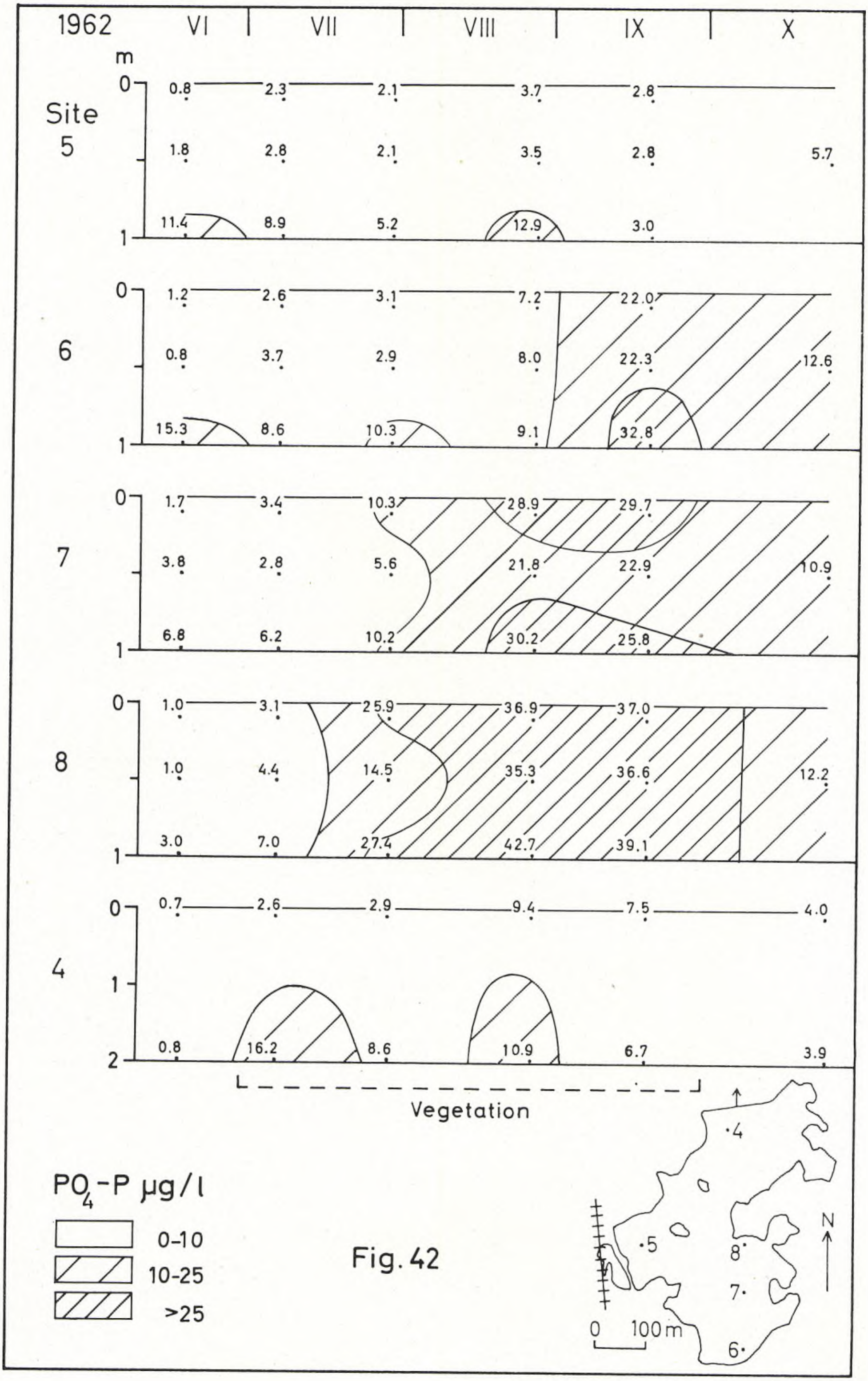

1962
VI
VII
VIII
IX
X
m
Site
5
0.8 2.3 2.1 3.7 2.8
1.8 2.8 2.1 3.5 2.8 5.7
11.4 8.9 5.2 12.9 3.0
6
1.2 2.6 3.1 7.2 22.0
0.8 3.7 2.9 8.0 22.3 12.6
15.3 8.6 10.3 9.1 32.8
7
1.7 3.4 10.3 28.9 29.7
3.8 2.8 5.6 21.8 22.9 10.9
6.8 6.2 10.2 30.2 25.8
8
1.0 3.1 25.9 36.9 37.0
1.0 4.4 14.5 35.3 36.6 12.2
3.0 7.0 27.4 42.7 39.1
4
0.7 2.6 2.9 9.4 7.5 4.0
0.8 16.2 8.6 10.9 6.7 3.9
0
1
2
Vegetation
PO$_4$-P µg/l
0-10
10-25
>25
4
5
8
7
6
N
0
100 m

Fig. 42

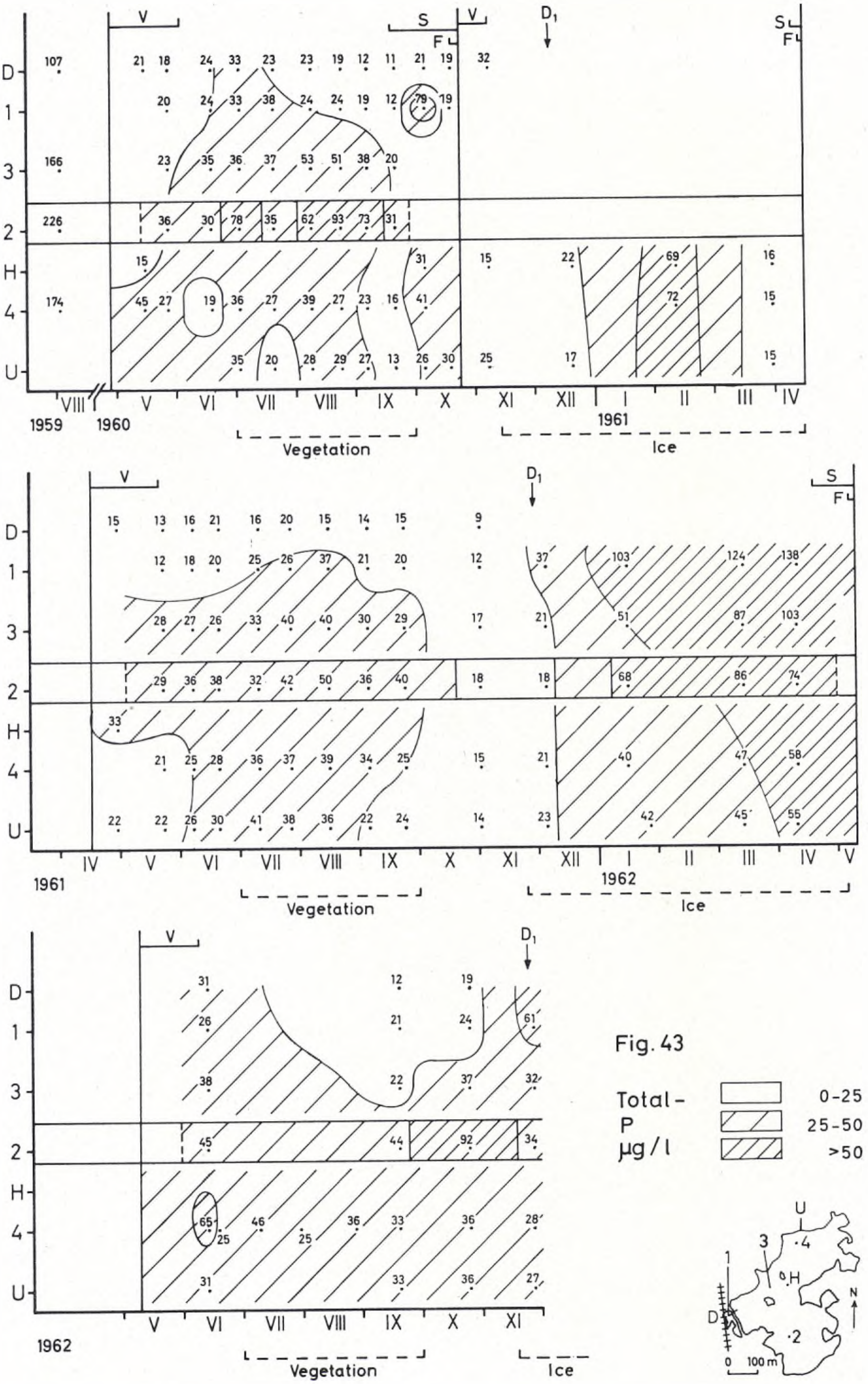

D
1
3
2
H
4
U
V
S
F
D1
VIII
V
VI
VII
VIII
IX
X
XI
XII
I
II
III
IV
1959
1960
1961
1962
Vegetation
Ice
Total-P µg/l
0-25
25-50
>50
U
3
4
1
H
D
2
N
0
100 m

Fig. 43

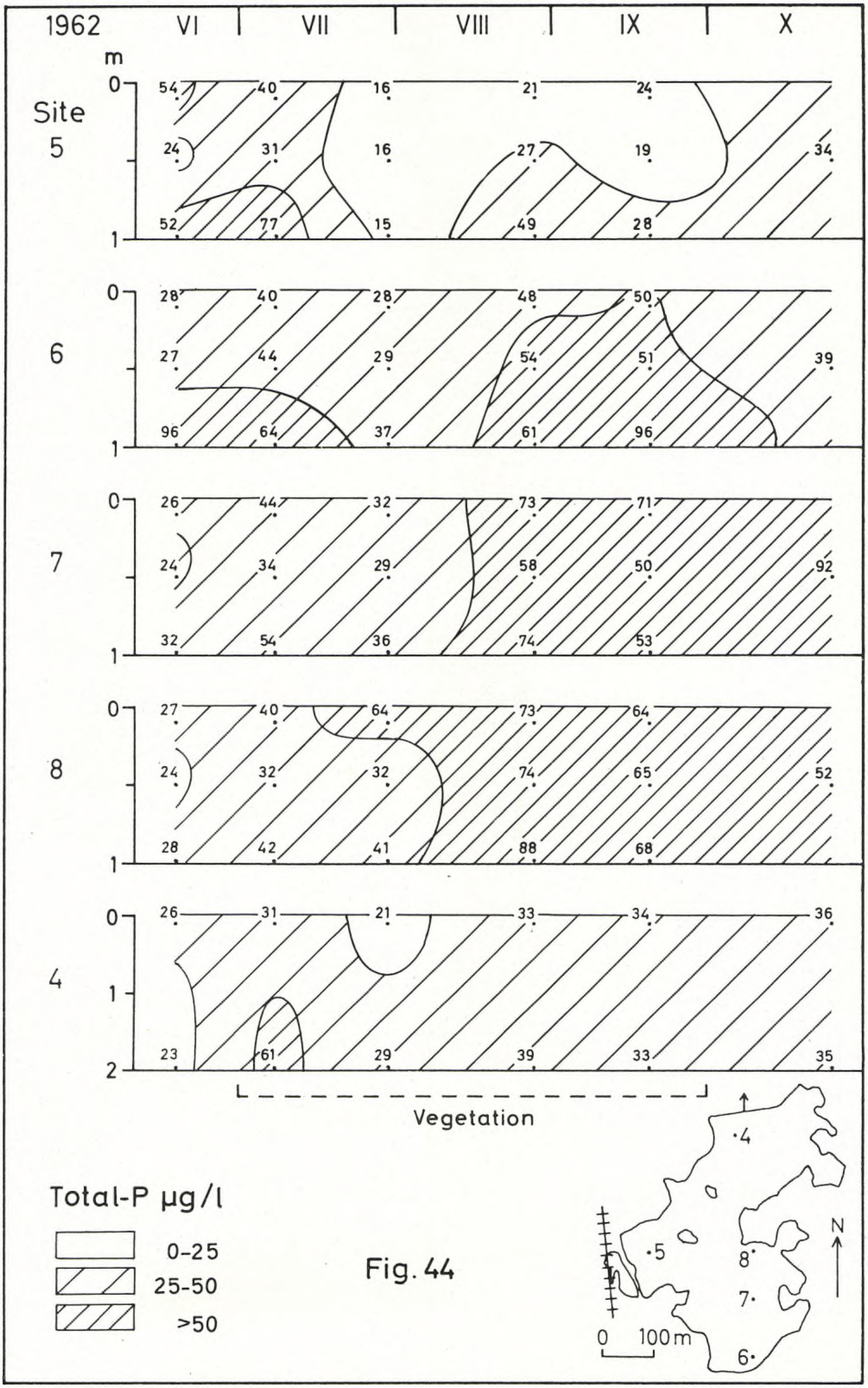

1962
VI
VII
VIII
IX
X
m
Site
5
0
1
54 40 16 21 24
24 31 16 27 19 34
52 77 15 49 28
6
0
1
28 40 28 48 50
27 44 29 54 51 39
96 64 37 61 96
7
0
1
26 44 32 73 71
24 34 29 58 50 92
32 54 36 74 53
8
0
1
27 40 64 73 64
24 32 32 74 65 52
28 42 41 88 68
4
0
1
2
26 31 21 33 34 36
23 61 29 39 33 35
Vegetation
Total-P µg/l
0–25
25–50
>50
·4
·5
8·
7·
6·
N
0
100 m

Fig. 44

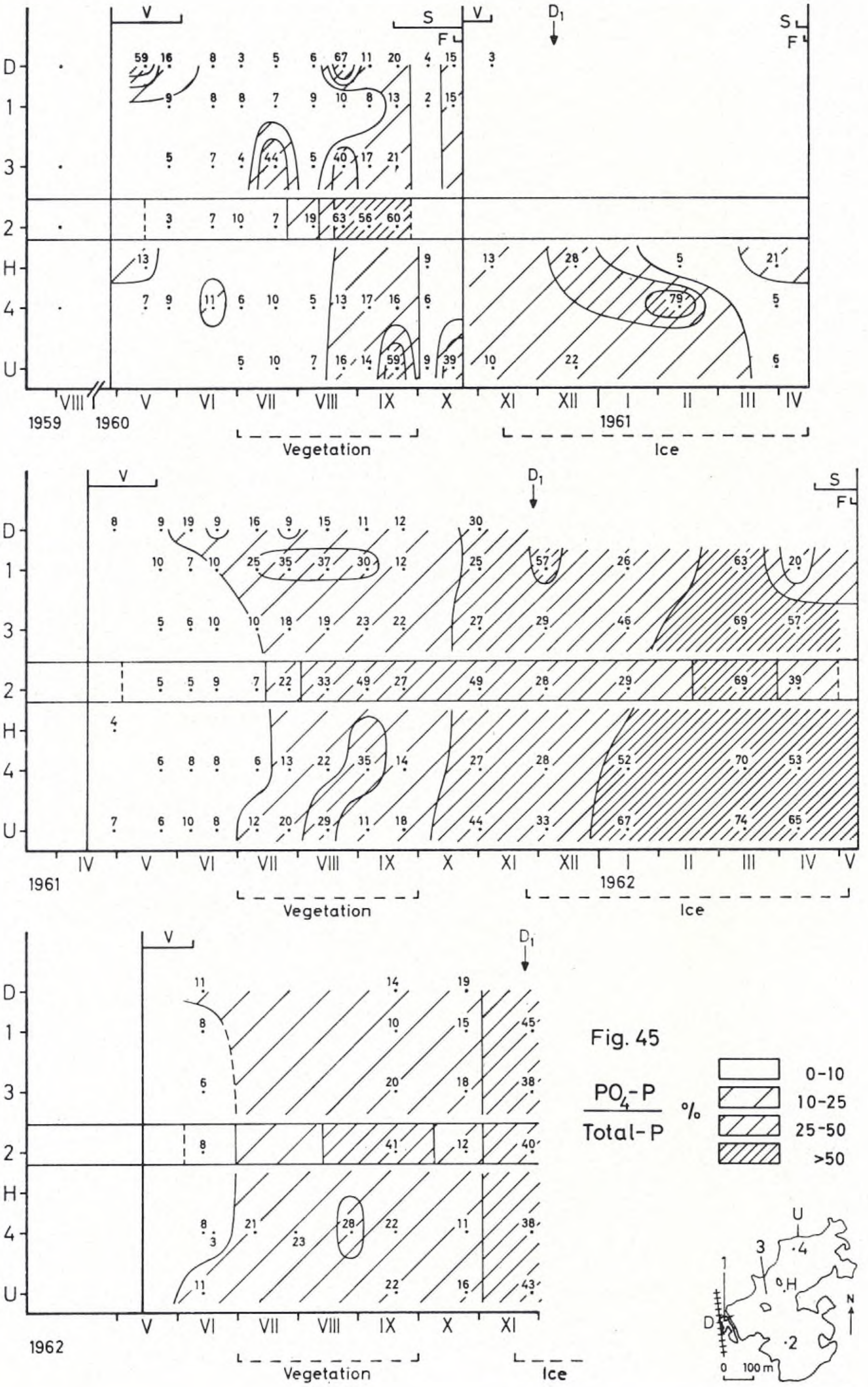

D
1
3
2
H
4
U
V
S
F
D1
VIII
V
VI
VII
VIII
IX
X
XI
XII
I
II
III
IV
1959
1960
1961
1962
Vegetation
Ice
PO4-P / Total-P %
0-10
10-25
25-50
>50
U
3
4
1
H
D
2
N
0 100 m

Fig. 45

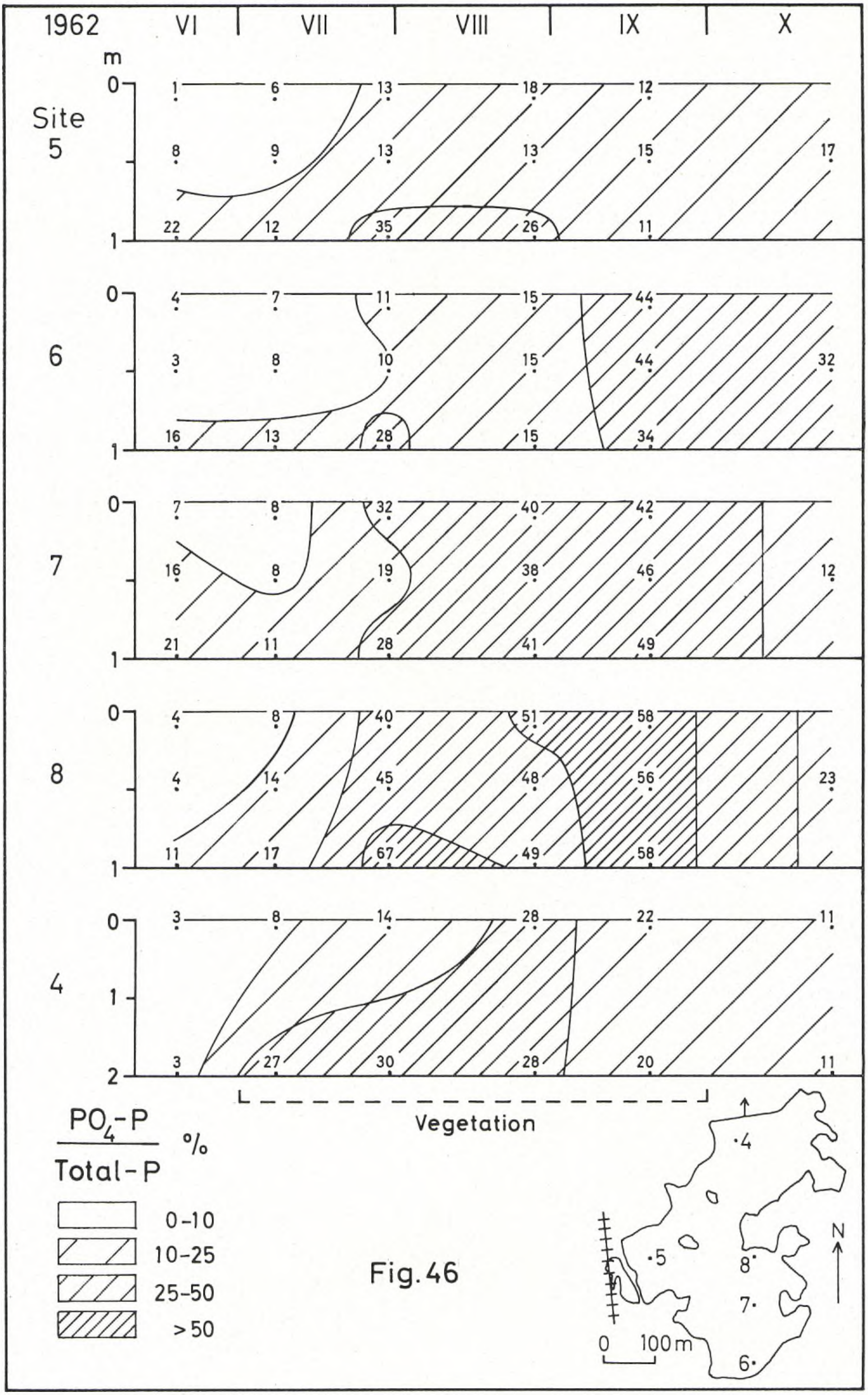

1962
VI
VII
VIII
IX
X
m
Site 5
0
1
1 6 13 18 12
8 9 13 13 15 17
22 12 35 26 11
6
0
1
4 7 11 15 44
3 8 10 15 44 32
16 13 28 15 34
7
0
1
7 8 32 40 42
16 8 19 38 46 12
21 11 28 41 49
8
0
1
4 8 40 51 58
4 14 45 48 56 23
11 17 67 49 58
4
0
1
2
3 8 14 28 22 11
3 27 30 28 20 11
Vegetation
$\frac{PO_4\text{-}P}{Total\text{-}P}$ %
0-10
10-25
25-50
>50
N
0 100 m
4
5
8
7
6

Fig. 46

(b) *Nitrogen.*

Data on the various nitrogen fractions are presented in the following Figures: Fig. 47 for ammonium-N, Figs. 48 and 49 for nitrite-N, Figs. 50 and 51 for nitrate-N, Figs. 52 and 53 for total-N, and the proportion of organically bound nitrogen, calculated from these data, in Fig. 54.

Analysis of ammonium-N has been done only during summer 1962. The results show that after filling there are larger amounts than later in the summer. In the SE bay the amounts are somewhat larger than in the other parts of the pond.

Analysis of nitrite-N has been done from late September 1961 onwards. Thus they cover the period when the pond was water-filled even during the winter. The only small increase which was recorded was at site 1, which is separated from the rest of the pond and therefore also from the aeration tube. Otherwise, as expected, the contents are low and sometimes undetectable.

Contents of nitrate-N are low in the summer and sometimes undetectable. At site 6, near the springs, somewhat higher values can be recorded for the bottom water. In winter the contents increase. The spring water is rich in nitrogen (see below under total-N), of which a considerable part is nitrate-N. The value varied between 102 and 2,930 with a mean value of 670 µg nitrate-N per litre.

Total-N values from 1959 up to June 13 1962 are probably too low (see p. 5). If the total-N content does not vary too much from year to year during the period of the investigation, it seems from the values after June 13 1962 that the values from LOHAMMAR's method should be multiplied by a factor of about 2. Only one isoplete has been drawn in Fig. 52, but in Fig. 53, where all values except those from the first sampling occasion have been obtained from analysis after Kjeldahl digestion, further isopletes have been drawn. Fig. 53 shows that the SE bay has somewhat higher total-N than the rest of the pond, during the vegetation period. Spring water contains 886 µg per litre on average, according to analyses by LOHAMMAR's method. The values vary between 150 and 3,030 µg total-N per litre.

The proportion of organically bound nitrogen expressed as a percentage of total-N has been calculated only for sites 4—8 during summer 1962 (see above section on total-N values). The lowest values were observed at site 5. In the main, *c.* 95 % of total-N is bound in an organic form.

(c) *Nitrogen/phosphorus relations.*

In Figs. 55 and 56 the ratio between total-N and total-P, calculated from data given earlier, is shown. In Fig. 55 the total-N values which are erroneously too low have been used (see above). The ratios given should be multiplied by about 2. Fig. 56 shows that there is a change in the relation between nitrogen and phosphorus during the first half of the vegetation period. This

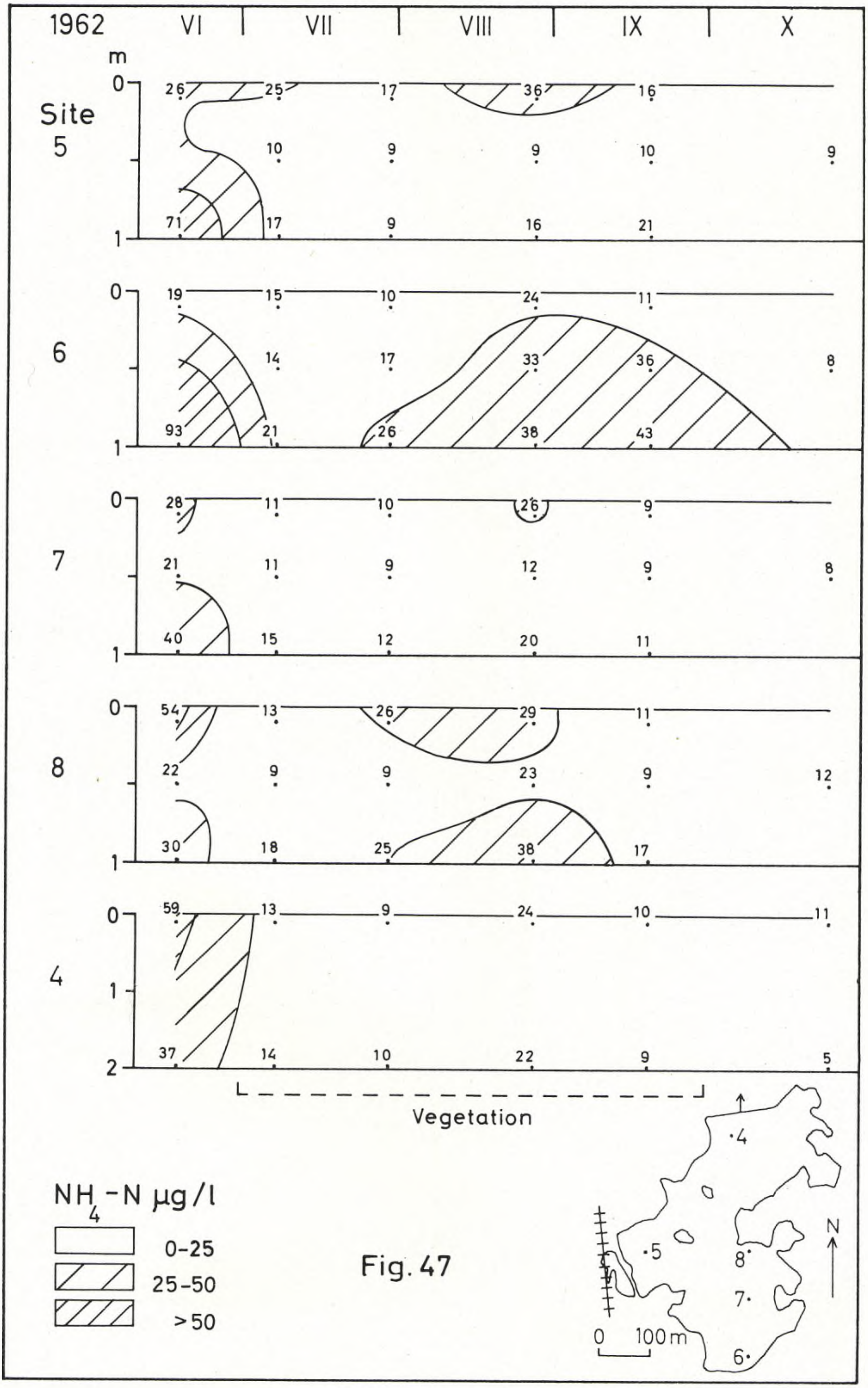

1962
VI
VII
VIII
IX
X
m
Site 5
0
1
26 25 17 36 16
10 9 9 10 9
71 17 9 16 21
6
19 15 10 24 11
14 17 33 36 8
93 21 26 38 43
7
28 11 10 26 9
21 11 9 12 9 8
40 15 12 20 11
8
54 13 26 29 11
22 9 9 23 9 12
30 18 25 38 17
4
2
59 13 9 24 10 11
37 14 10 22 9 5
Vegetation
NH$_4$-N µg/l
0-25
25-50
>50
·4
·5
8·
7·
6·
N
0
100 m

Fig. 47

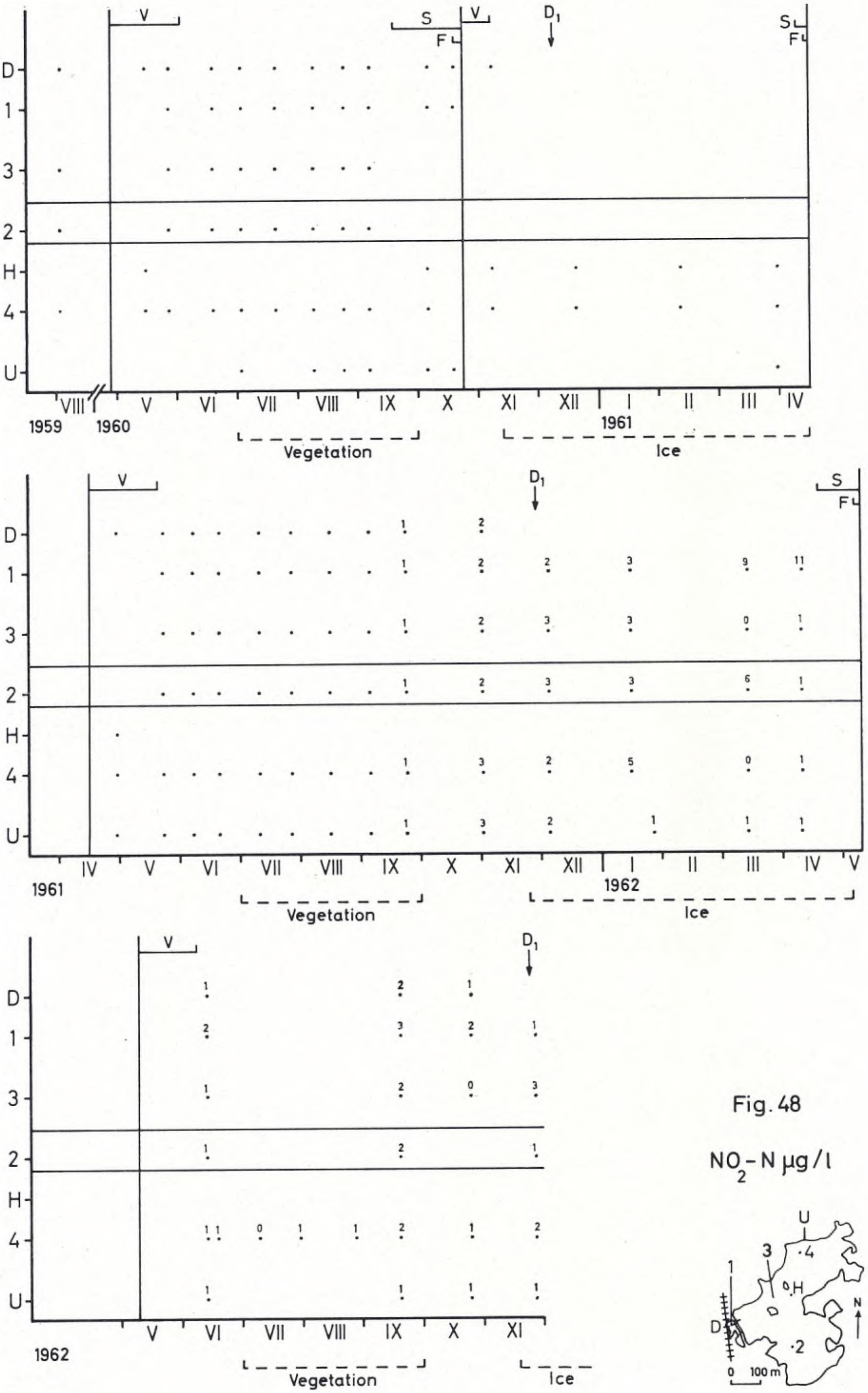


Fig. 48

NO₂-N µg/l

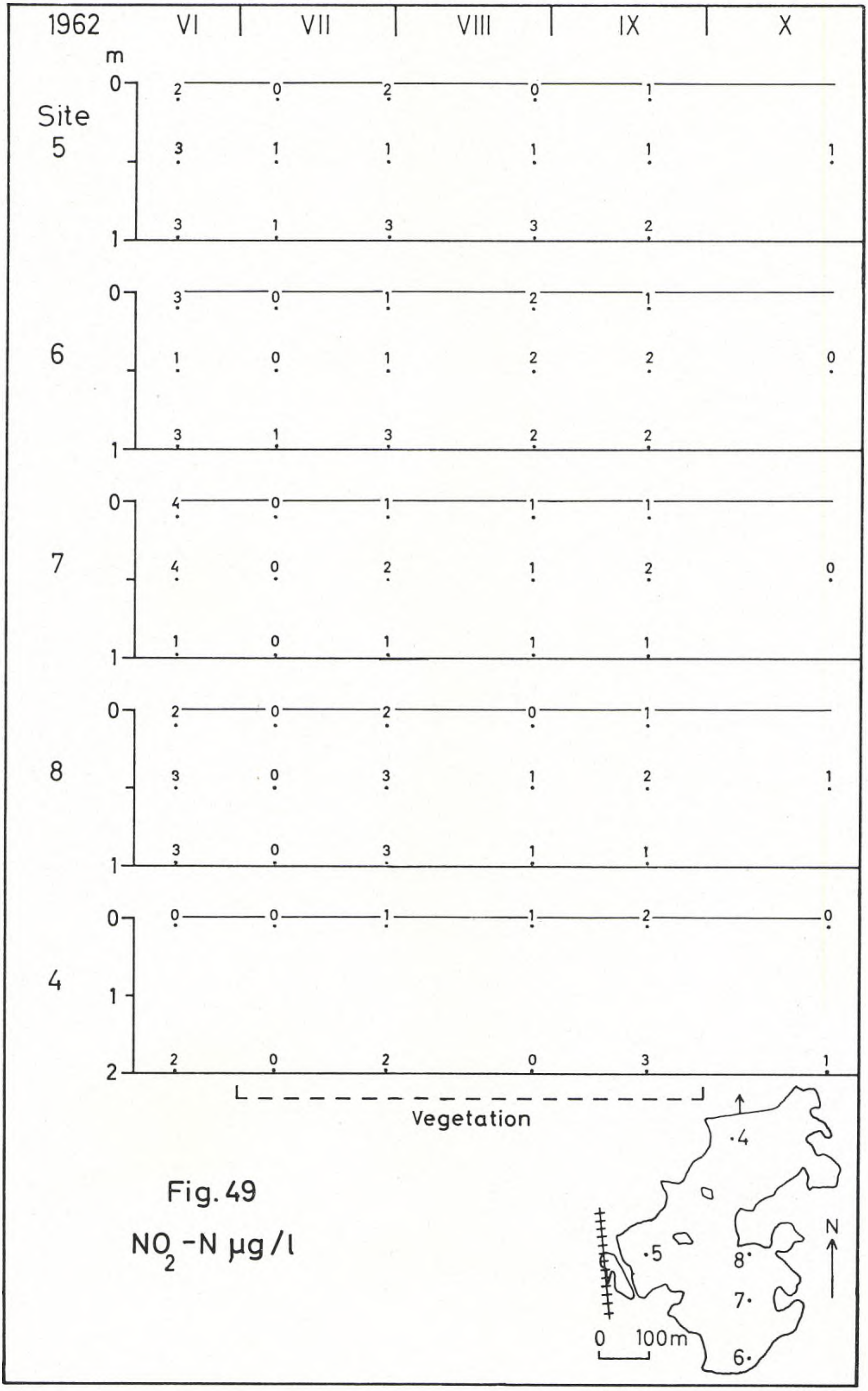


Fig. 49

NO_2-N µg/l

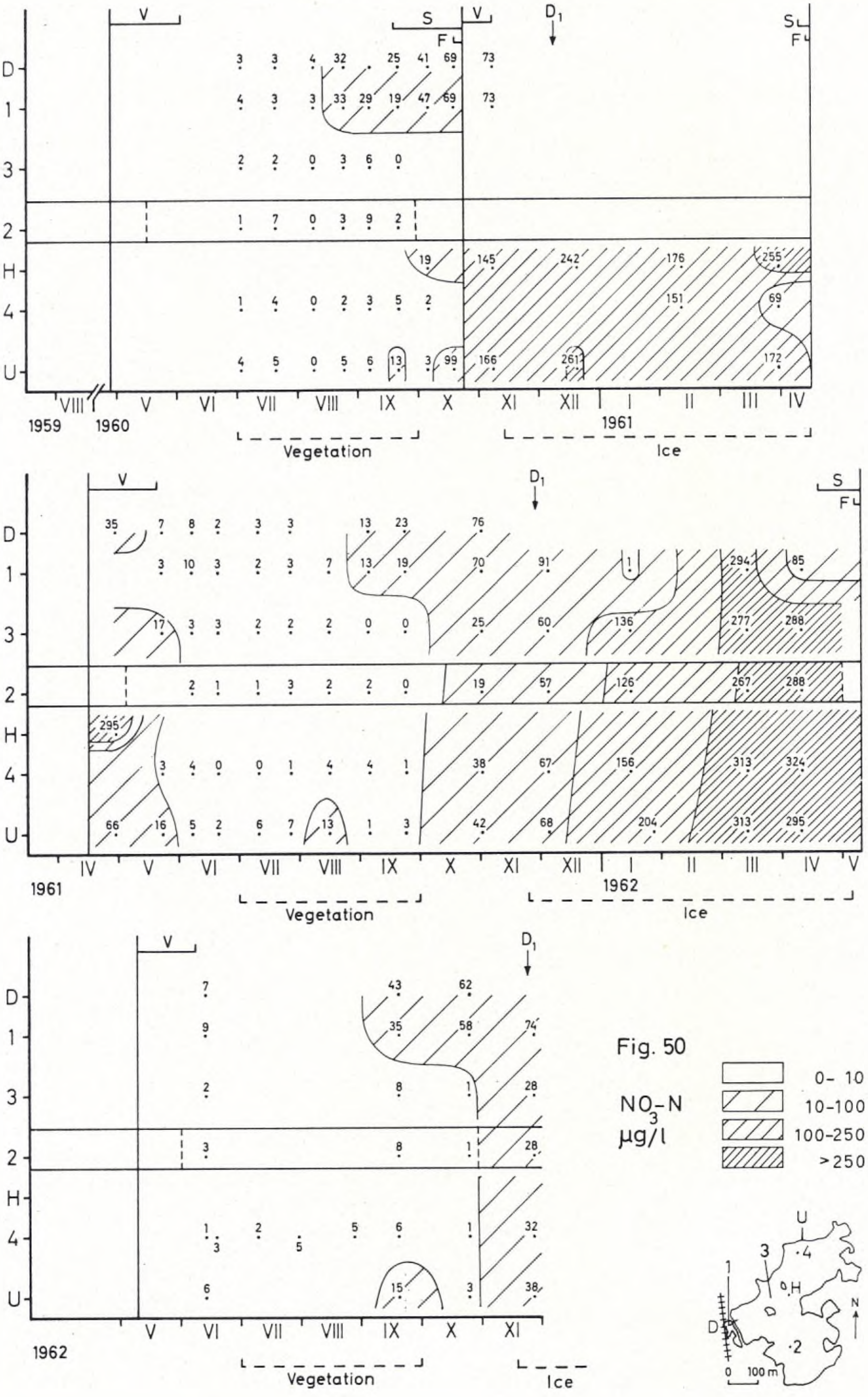

D
1
3
2
H
4
U
V
S
F
D1
3 3 4 32 25 41 69 73
4 3 3 33 29 19 47 69 73
2 2 0 3 6 0
1 7 0 3 9 2
19 145 242 176 255
1 4 0 2 3 5 2 151 69
4 5 0 5 6 13 3 99 166 261 172
VIII V VI VII VIII IX X XI XII I II III IV
1959 1960 1961
Vegetation
Ice
35 7 8 2 3 3 13 23 76
3 10 3 2 3 7 13 19 70 91 1 294 85
17 3 3 2 2 2 0 0 25 60 136 277 288
2 1 1 3 2 2 0 19 57 126 267 288
295
3 4 0 0 1 4 4 1 38 67 156 313 324
66 16 5 2 6 7 13 1 3 42 68 204 313 295
IV V VI VII VIII IX X XI XII I II III IV V
1961 1962
7 43 62
9 35 58 74
2 8 1 28
3 8 1 28
1 3 2 5 5 6 1 32
6 15 3 38
V VI VII VIII IX X XI
1962
NO3-N µg/l
0- 10
10-100
100-250
>250
U
3
4
1
H
N
D
2
0 100 m

Fig. 50

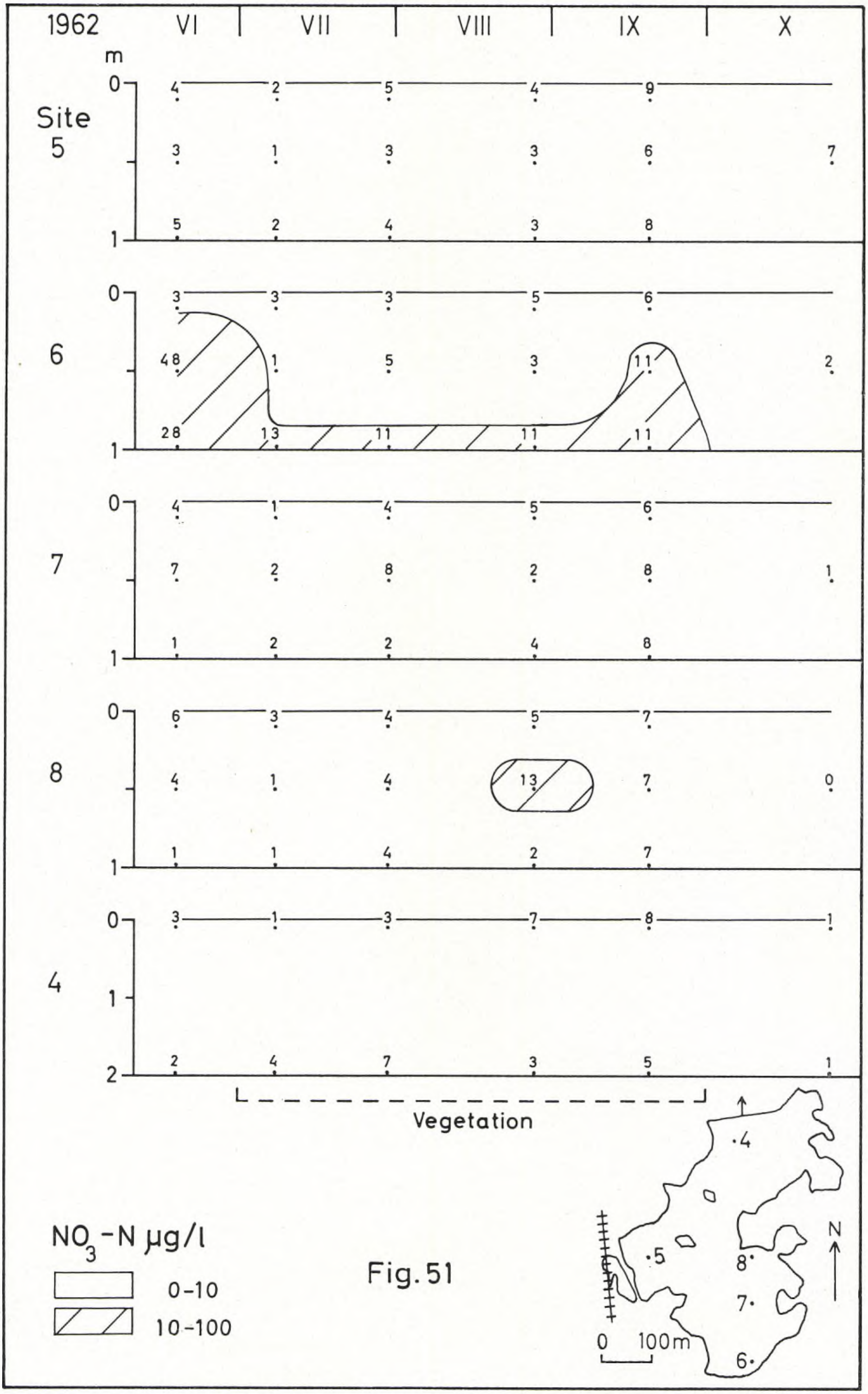

1962
VI
VII
VIII
IX
X
m
Site 5
0
1
4 2 5 4 9
3 1 3 3 6 7
5 2 4 3 8
6
0
1
3 3 3 5 6
48 1 5 3 11 2
28 13 11 11 11
7
0
1
4 1 4 5 6
7 2 8 2 8 1
1 2 2 4 8
8
0
1
6 3 4 5 7
4 1 4 13 7 0
1 1 4 2 7
4
0
1
2
3 1 3 7 8 1
2 4 7 3 5 1
Vegetation
NO3-N µg/l
0-10
10-100
·4
·5
8·
7·
6·
N
0
100m

Fig. 51

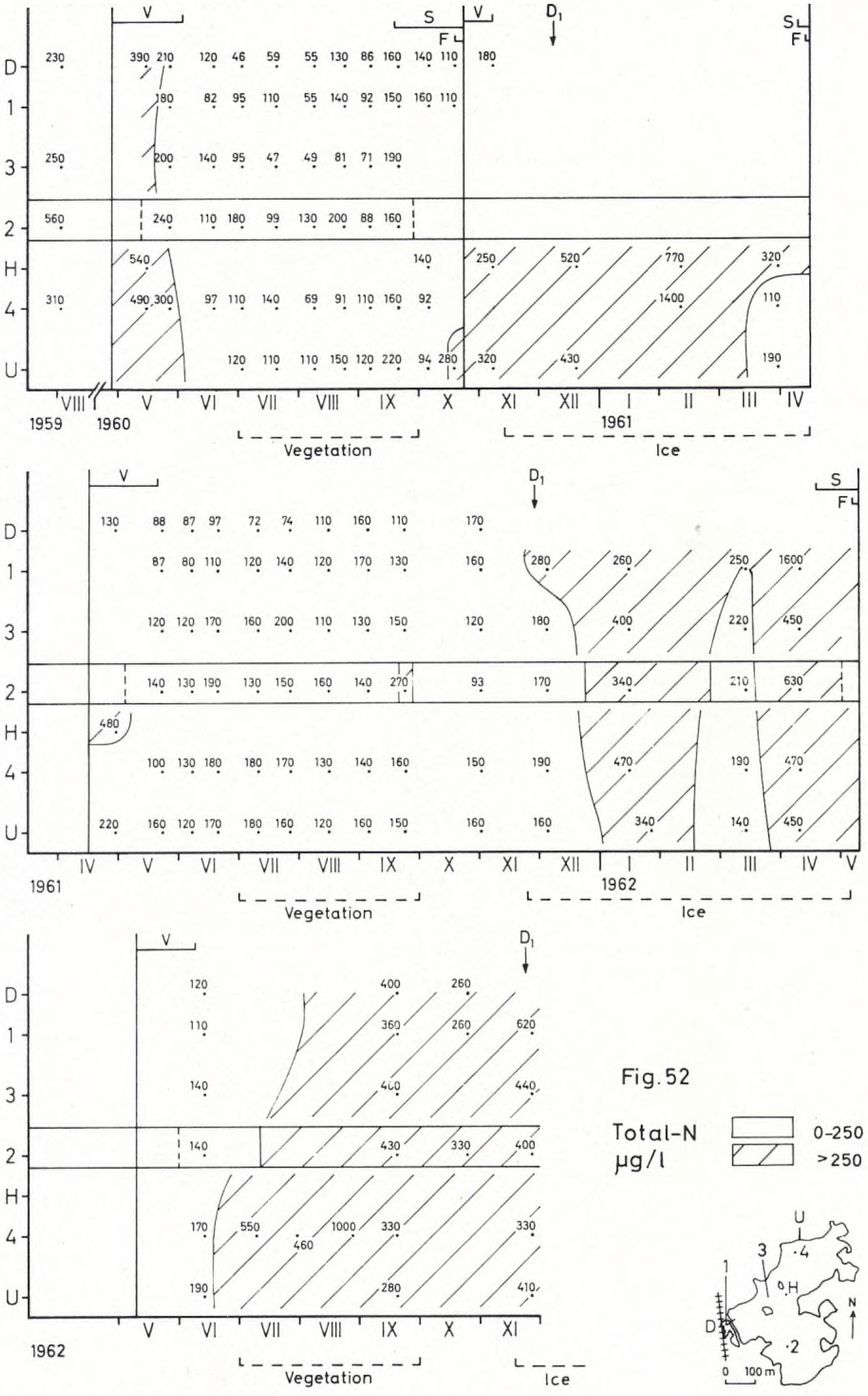

V
S
F
D₁
D
1
3
2
H
4
U
230 390 210 120 46 59 55 130 86 160 140 110 180
180 82 95 110 55 140 92 150 160 110
250 200 140 95 47 49 81 71 190
560 240 110 180 99 130 200 88 160
540 140 250 520 770 320
310 490 300 97 110 140 69 91 110 160 92 1400 110
120 110 110 150 120 220 94 280 320 430 190
VIII V VI VII VIII IX X XI XII I II III IV
1959 1960 1961
Vegetation
Ice
130 88 87 97 72 74 110 160 110 170
87 80 110 120 140 120 170 130 160 280 260 250 1600
120 120 170 160 200 110 130 150 120 180 400 220 450
140 130 190 130 150 160 140 270 93 170 340 210 630
480
100 130 180 180 170 130 140 160 150 190 470 190 470
220 160 120 170 180 160 120 160 150 160 160 340 140 450
IV V VI VII VIII IX X XI XII I II III IV V
1961 1962
Vegetation
Ice
120 400 260
110 360 260 620
140 400 440
140 430 330 400
170 550 460 1000 330 330
190 280 410
V VI VII VIII IX X XI
1962
Vegetation
Ice
Total-N
µg/l
0-250
>250
U
3
4
1
H
D
2
N
0 100 m

Fig. 52

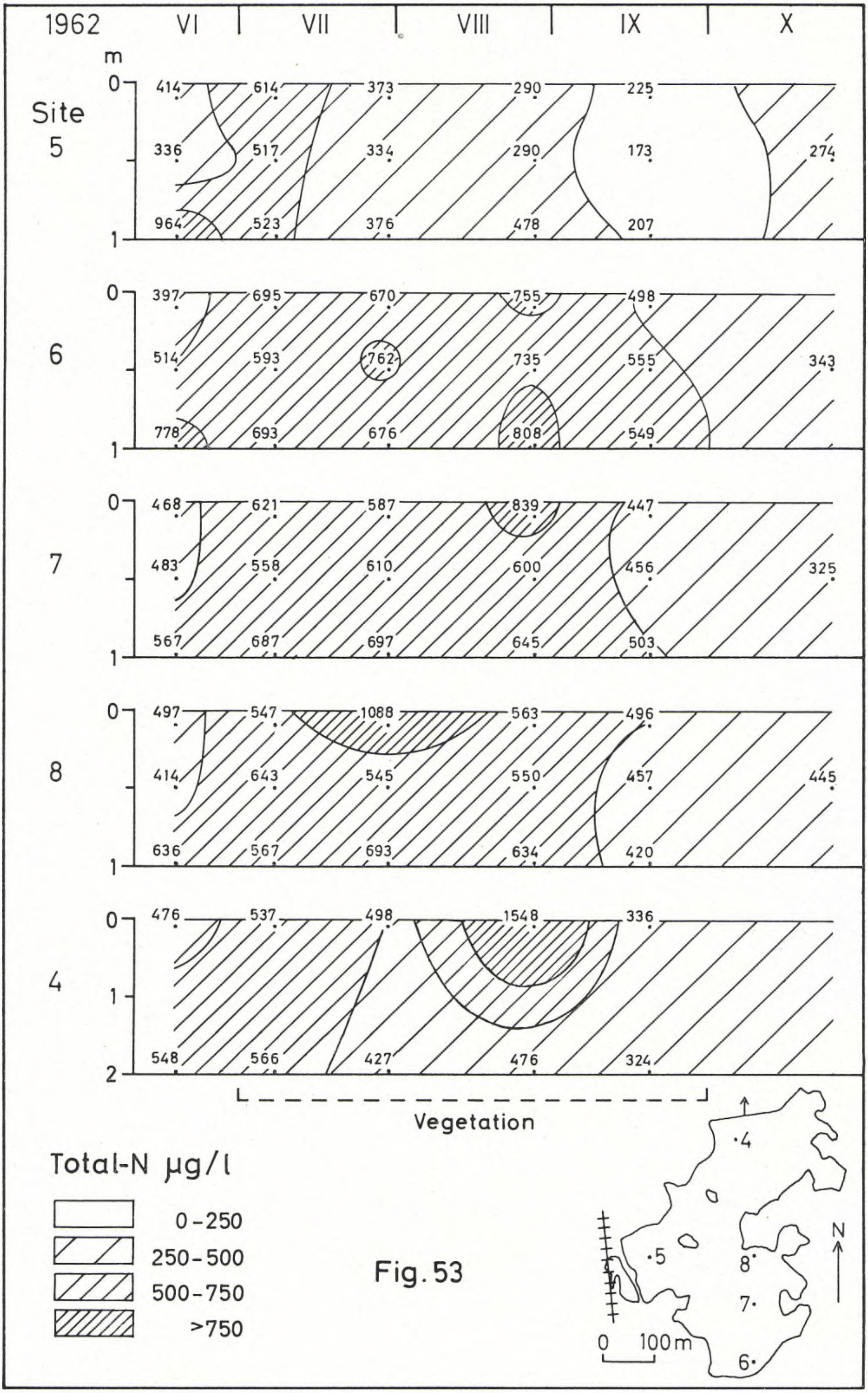

1962
VI
VII
VIII
IX
X
m
Site
5
0
414 614 373 290 225
336 517 334 290 173 274
964 523 376 478 207
1
6
0
397 695 670 755 498
514 593 762 735 555 343
778 693 676 808 549
1
7
0
468 621 587 839 447
483 558 610 600 456 325
567 687 697 645 503
1
8
0
497 547 1088 563 496
414 643 545 550 457 445
636 567 693 634 420
1
4
0
476 537 498 1548 336
1
548 566 427 476 324
2
Vegetation
Total-N µg/l
0-250
250-500
500-750
>750
·4
·5
8·
7·
6·
N
0 100m

Fig. 53

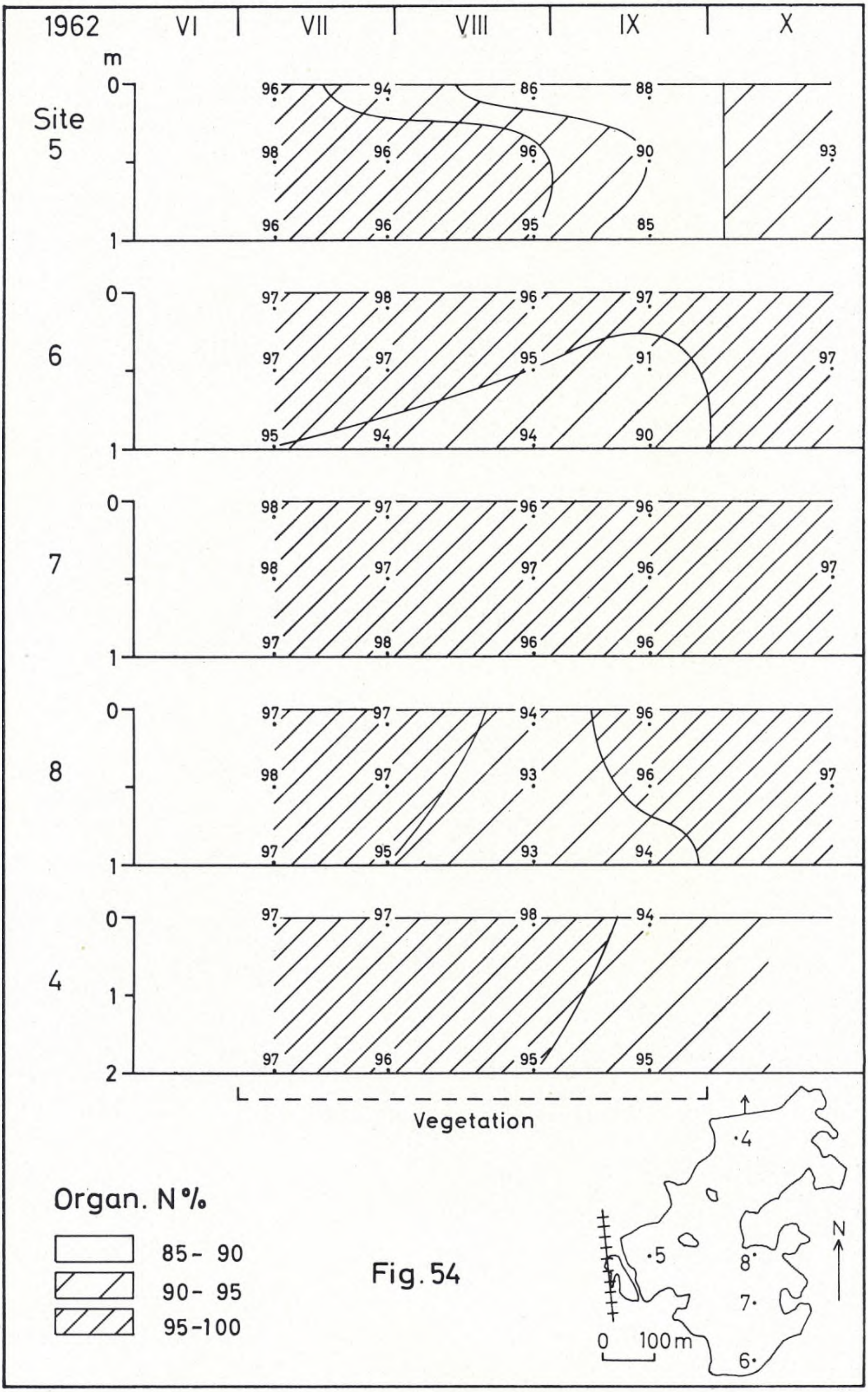

1962
VI
VII
VIII
IX
X
m
Site 5
0
1
96 94 86 88
98 96 96 90 93
96 96 95 85
6
0
1
97 98 96 97
97 97 95 91 97
95 94 94 90
7
0
1
98 97 96 96
98 97 97 96 97
97 98 96 96
8
0
1
97 97 94 96
98 97 93 96 97
97 95 93 94
4
0
1
2
97 97 98 94
97 96 95 95
Vegetation
Organ. N %
85- 90
90- 95
95-100
·4
·5
8·
7·
6·
N
0 100 m

Fig. 54

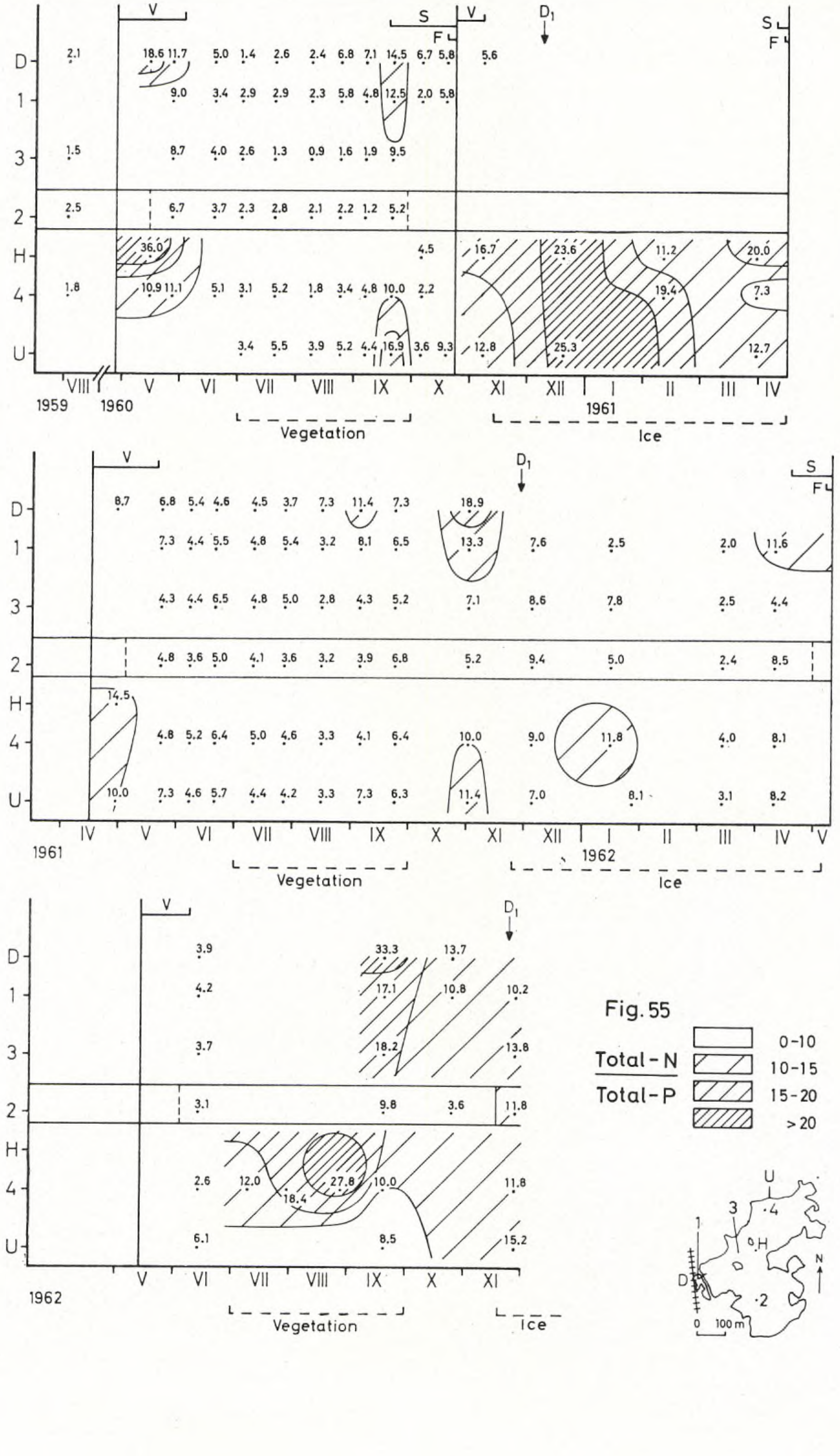

V
S
F
D₁
D
1
3
2
H
4
U
2.1 18.6 11.7 5.0 1.4 2.6 2.4 6.8 7.1 14.5 6.7 5.8 5.6
9.0 3.4 2.9 2.9 2.3 5.8 4.8 12.5 2.0 5.8
1.5 8.7 4.0 2.6 1.3 0.9 1.6 1.9 9.5
2.5 6.7 3.7 2.3 2.8 2.1 2.2 1.2 5.2
36.0 4.5 16.7 23.6 11.2 20.0
1.8 10.9 11.1 5.1 3.1 5.2 1.8 3.4 4.8 10.0 2.2 19.4 7.3
3.4 5.5 3.9 5.2 4.4 16.9 3.6 9.3 12.8 25.3 12.7
VIII V VI VII VIII IX X XI XII I II III IV
1959 1960 1961
Vegetation
Ice
8.7 6.8 5.4 4.6 4.5 3.7 7.3 11.4 7.3 18.9
7.3 4.4 5.5 4.8 5.4 3.2 8.1 6.5 13.3 7.6 2.5 2.0 11.6
4.3 4.4 6.5 4.8 5.0 2.8 4.3 5.2 7.1 8.6 7.8 2.5 4.4
4.8 3.6 5.0 4.1 3.6 3.2 3.9 6.8 5.2 9.4 5.0 2.4 8.5
14.5
4.8 5.2 6.4 5.0 4.6 3.3 4.1 6.4 10.0 9.0 11.8 4.0 8.1
10.0 7.3 4.6 5.7 4.4 4.2 3.3 7.3 6.3 11.4 7.0 8.1 3.1 8.2
IV V VI VII VIII IX X XI XII I II III IV V
1961 1962
Vegetation
Ice
3.9 33.3 13.7
4.2 17.1 10.8 10.2
3.7 18.2 13.8
3.1 9.8 3.6 11.8
2.6 12.0 18.4 27.8 10.0 11.8
6.1 8.5 15.2
V VI VII VIII IX X XI
1962
Vegetation
Ice
Total-N
Total-P
0-10
10-15
15-20
>20
U
3
4
1
H
D
2
N
0 100 m

Fig. 55

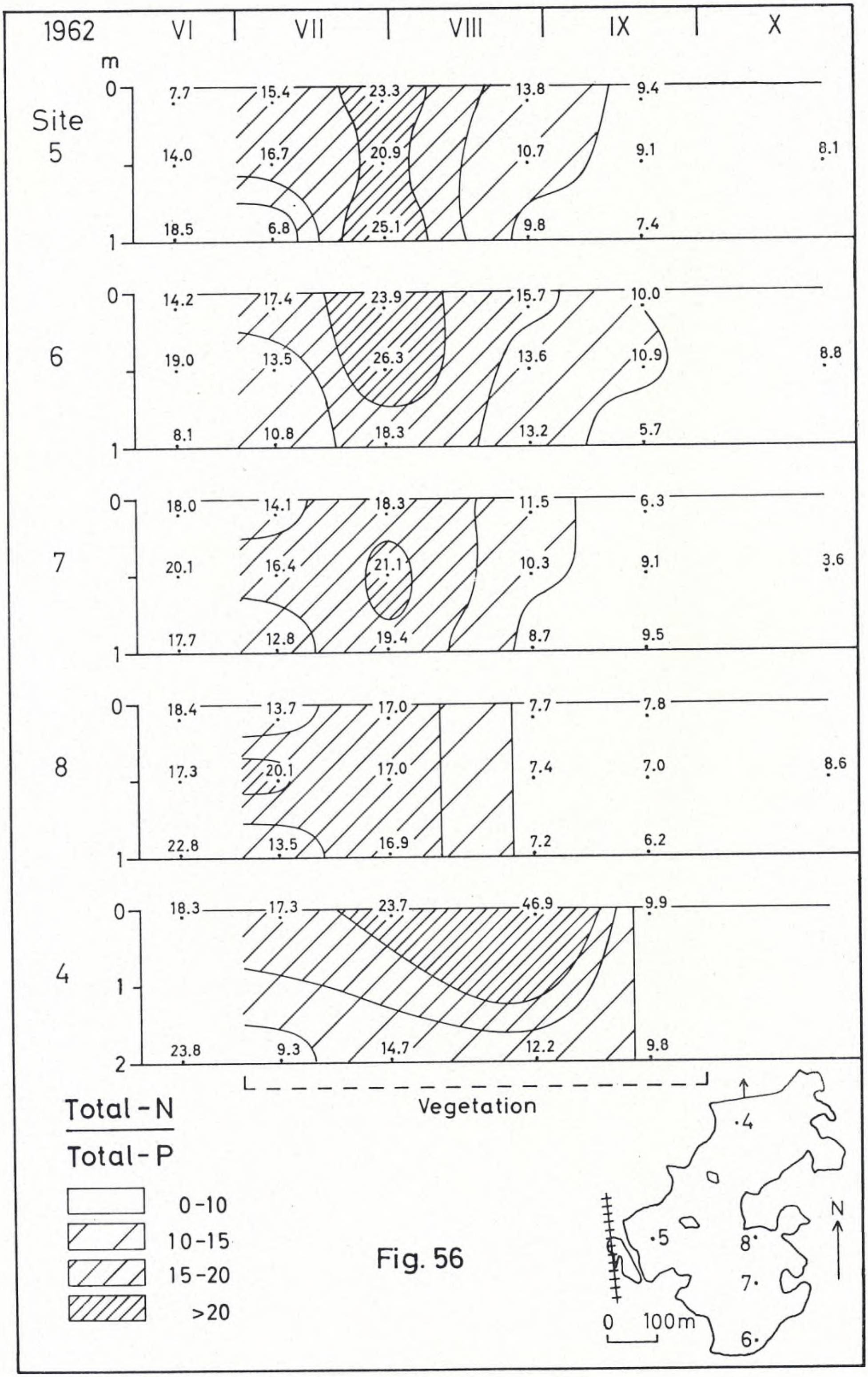

1962
VI
VII
VIII
IX
X
m
Site 5
0
1
7.7
15.4
23.3
13.8
9.4
14.0
16.7
20.9
10.7
9.1
8.1
18.5
6.8
25.1
9.8
7.4
6
14.2
17.4
23.9
15.7
10.0
19.0
13.5
26.3
13.6
10.9
8.8
8.1
10.8
18.3
13.2
5.7
7
18.0
14.1
18.3
11.5
6.3
20.1
16.4
21.1
10.3
9.1
3.6
17.7
12.8
19.4
8.7
9.5
8
18.4
13.7
17.0
7.7
7.8
17.3
20.1
17.0
7.4
7.0
8.6
22.8
13.5
16.9
7.2
6.2
4
18.3
17.3
23.7
46.9
9.9
23.8
9.3
14.7
12.2
9.8
2
Vegetation
Total-N
Total-P
0-10
10-15
15-20
>20
N
0 100m
4
5
8
7
6

Fig. 56

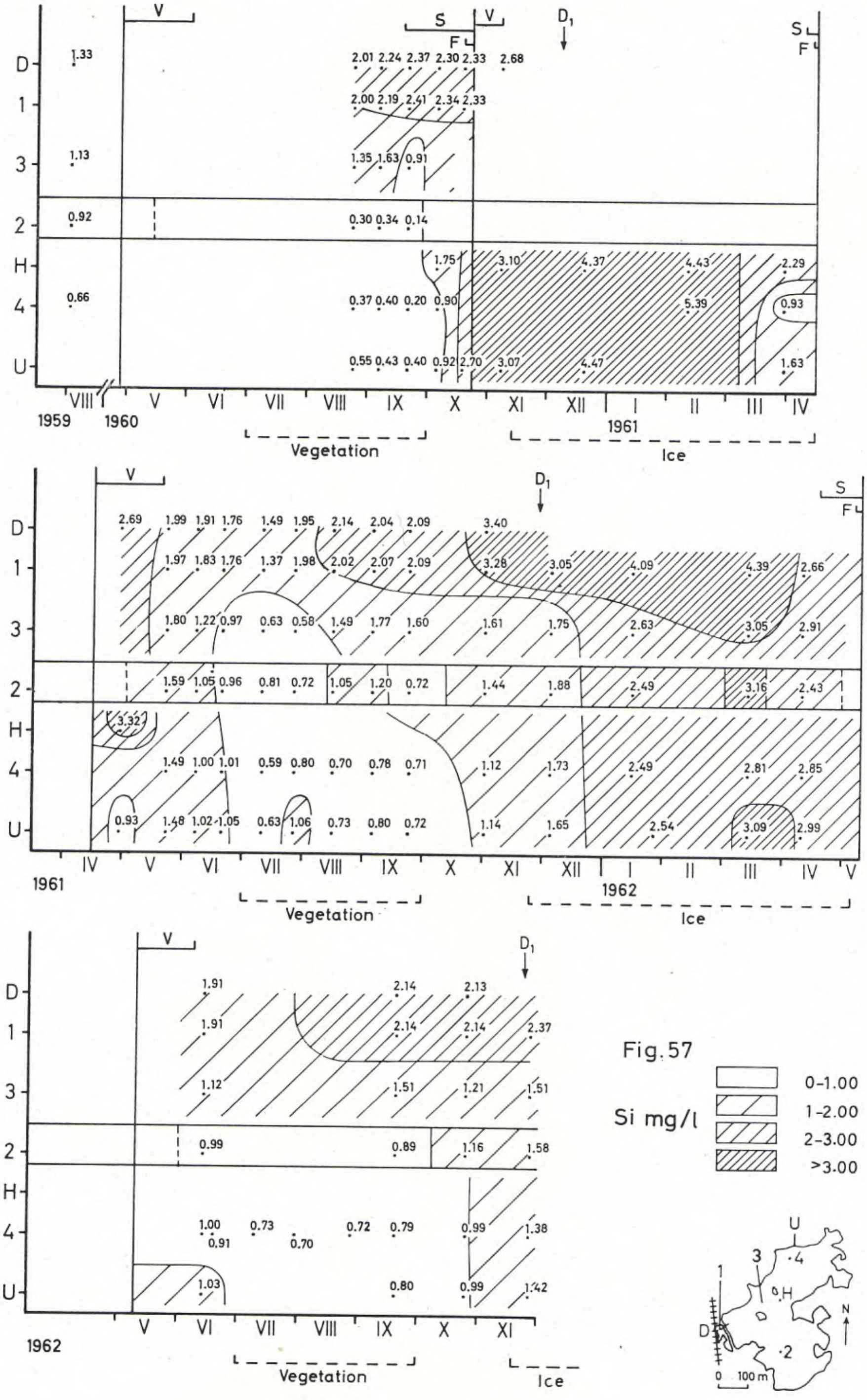

V
S
V
F
D1
S
F
D
1
3
2
H
4
U
1.33
2.01 2.24 2.37 2.30 2.33 2.68
2.00 2.19 2.41 2.34 2.33
1.13
1.35 1.63 0.91
0.92
0.30 0.34 0.14
1.75 3.10 4.37 4.43 2.29
0.66
0.37 0.40 0.20 0.90 5.39 0.93
0.55 0.43 0.40 0.92 2.70 3.07 4.47 1.63
VIII V VI VII VIII IX X XI XII I II III IV
1959 1960
1961
Vegetation
Ice
2.69 1.99 1.91 1.76 1.49 1.95 2.14 2.04 2.09 3.40
1.97 1.83 1.76 1.37 1.98 2.02 2.07 2.09 3.28 3.05 4.09 4.39 2.66
1.80 1.22 0.97 0.63 0.58 1.49 1.77 1.60 1.61 1.75 2.63 3.05 2.91
1.59 1.05 0.96 0.81 0.72 1.05 1.20 0.72 1.44 1.88 2.49 3.16 2.43
3.32
1.49 1.00 1.01 0.59 0.80 0.70 0.78 0.71 1.12 1.73 2.49 2.81 2.85
0.93 1.48 1.02 1.05 0.63 1.06 0.73 0.80 0.72 1.14 1.65 2.54 3.09 2.99
IV V VI VII VIII IX X XI XII I II III IV V
1961
1962
Vegetation
Ice
1.91 2.14 2.13
1.91 2.14 2.14 2.37
1.12 1.51 1.21 1.51
0.99 0.89 1.16 1.58
1.00 0.73 0.72 0.79 0.99 1.38
0.91 0.70
1.03 0.80 0.99 1.42
V VI VII VIII IX X XI
1962
Vegetation
Ice
Si mg/l
0-1.00
1-2.00
2-3.00
>3.00
U
3
4
1
H
D
2
N
0 100 m

Fig. 57

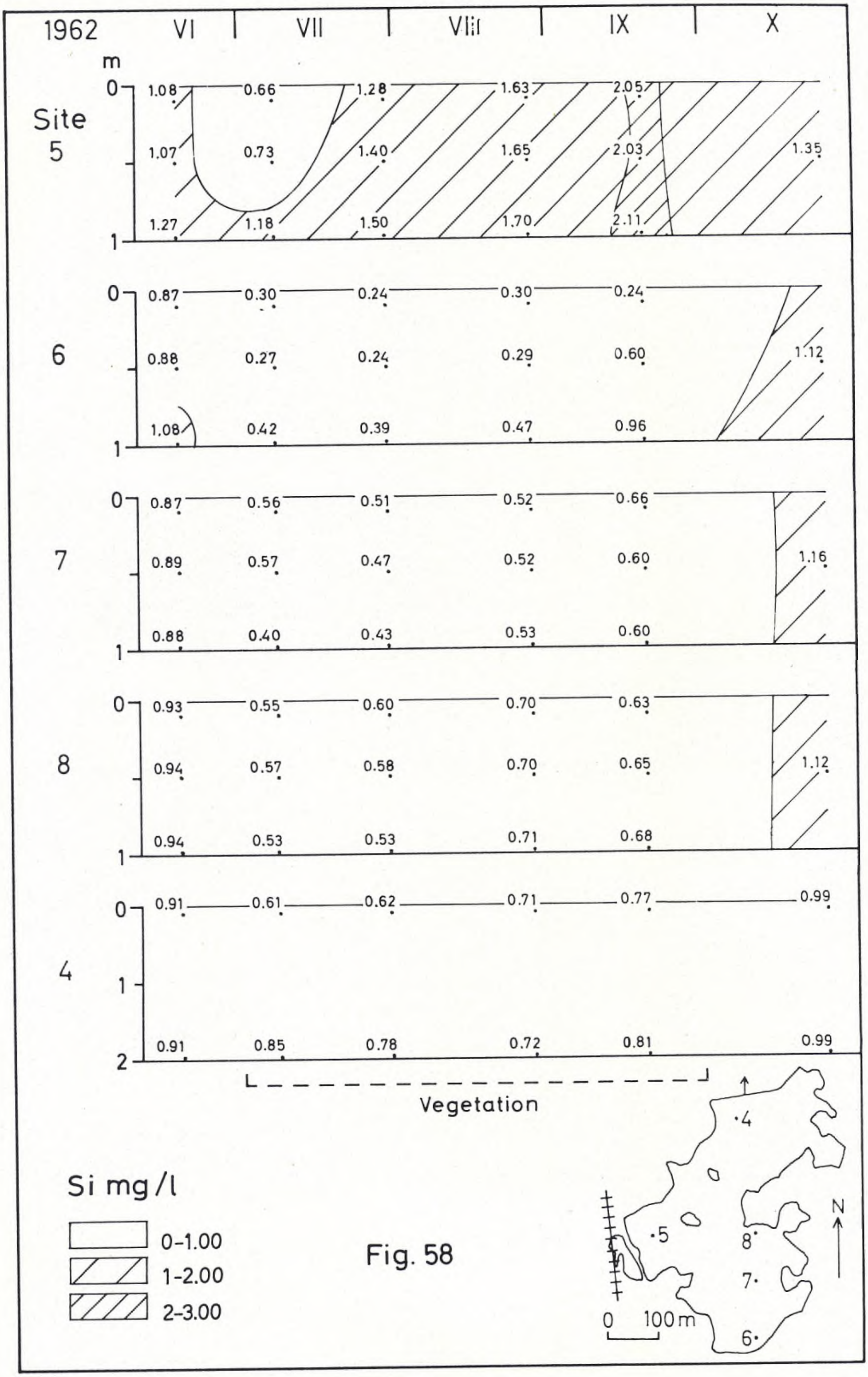

1962
VI
VII
VIII
IX
X
m
Site
5
0
1
1.08 0.66 1.28 1.63 2.05
1.07 0.73 1.40 1.65 2.03 1.35
1.27 1.18 1.50 1.70 2.11
6
0.87 0.30 0.24 0.30 0.24
0.88 0.27 0.24 0.29 0.60 1.12
1.08 0.42 0.39 0.47 0.96
7
0.87 0.56 0.51 0.52 0.66
0.89 0.57 0.47 0.52 0.60 1.16
0.88 0.40 0.43 0.53 0.60
8
0.93 0.55 0.60 0.70 0.63
0.94 0.57 0.58 0.70 0.65 1.12
0.94 0.53 0.53 0.71 0.68
4
0.91 0.61 0.62 0.71 0.77 0.99
2
0.91 0.85 0.78 0.72 0.81 0.99
Vegetation
Si mg/l
0-1.00
1-2.00
2-3.00
N
0 100 m
4
5
6
7
8

Fig. 58

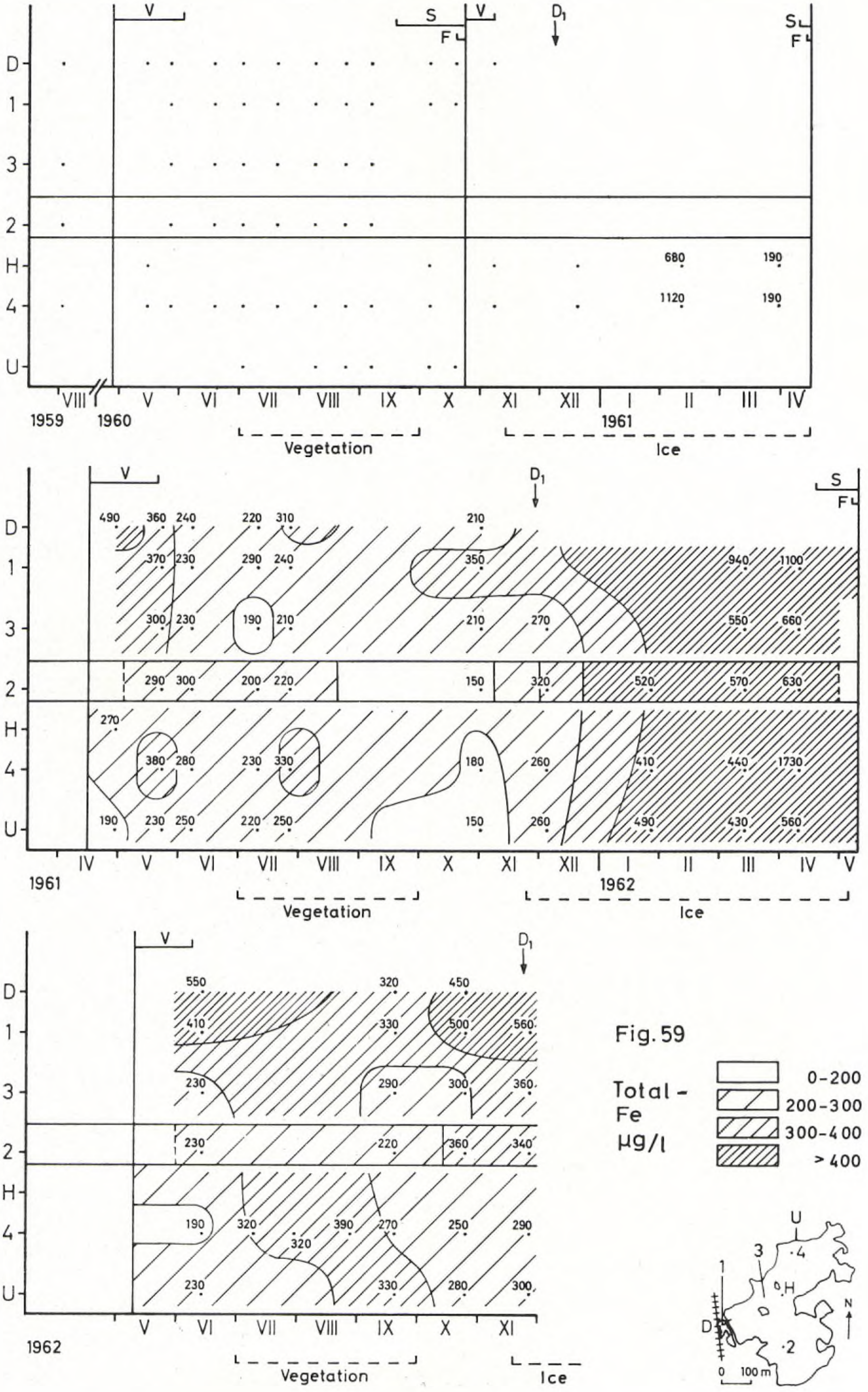


Fig. 59

D
1
3
2
H
4
U
V
S
F
D1
680
190
1120
190
VIII V VI VII VIII IX X XI XII I II III IV
1959
1960
1961
Vegetation
Ice
490 360 240 220 310 210
370 230 290 240 350 940 1100
300 230 190 210 210 270 550 660
290 300 200 220 150 320 520 570 630
270
380 280 230 330 180 260 410 440 1730
190 230 250 220 250 150 260 490 430 560
IV V VI VII VIII IX X XI XII I II III IV V
1961
1962
Vegetation
Ice
550 320 450
410 330 500 560
230 290 300 360
230 220 360 340
190 320 390 270 250 290
320
230 330 280 300
V VI VII VIII IX X XI
1962
Vegetation
Ice
Total - Fe µg/l
☐ 0-200
▨ 200-300
▨ 300-400
▨ > 400
U
3
4
1
H
D
2
N
0 100 m

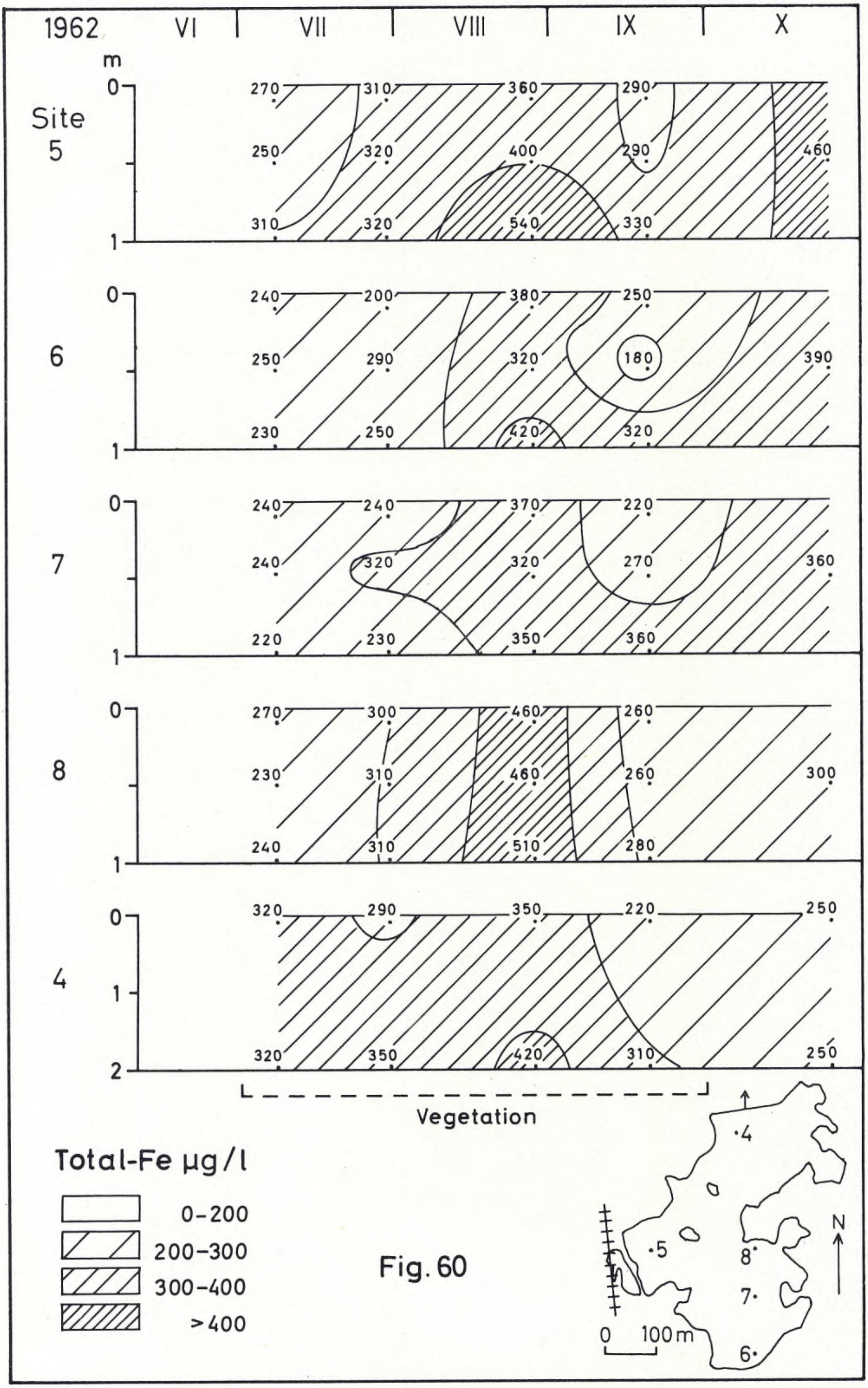

1962
VI
VII
VIII
IX
X
m
Site 5
0
1
270
310
360
290
250
320
400
290
460
310
320
540
330
6
240
200
380
250
250
290
320
180
390
230
250
420
320
7
240
240
370
220
240
320
320
270
360
220
230
350
360
8
270
300
460
260
230
310
460
260
300
240
310
510
280
4
2
320
290
350
220
250
320
350
420
310
250
Vegetation
Total-Fe µg/l
0-200
200-300
300-400
>400
·4
·5
8·
7·
6·
N
0
100 m

Fig. 60

is due mostly to an increase in total-N content. After that, total-N decreases and total-P increases, so that lower values obtain. No change can be detected in connection with the dying down of the vegetation.

(d) *Silicon.*

Data on silicon are given in Figs. 57 and 58. From these it is apparent that the content of the Dalälv water varies between 1.5 and 2.5 mg/l. during spring and summer. At the same time, the contents in the whole pond are lower and for the outflow stream there is a variation between 0.5 and 1.5 mg/l. (See p. 90.) In the winter the contents increase.

The mean silicon content of the spring water is 4.38 mg/l. The values vary between 2.81 and 5.89 mg Si per litre.

(e) *Iron.*

Analysis has been of total iron, and the data are presented in Figs. 59 and 60. There are no marked differences between the different sites, nor can any variation with time be detected during the summer. In the winter the contents increase considerably.

VI. Some major and minor constituents in relation to higher aquatic vegetation

1. Horizontal heterogeneity

The significance of the vegetation in ponds and lakes has been described from various aspects by NORDQUIST (1920), TITCOMB (1924), KLUGH (1926), FROHNE (1938), DE GRUCHY (1938), WILSON (1938), HOTCHKISS (1941), WELCH (1952), SEIDEL (1955), PENFOUND (1956) and SCHÄPERCLAUS (1961). One of these aspects is the significance of the vegetation for the chemical composition of the water, and this is dealt with in the present article. WELCH (1952, pp. 303—309) summarizes the most important direct and indirect relations of "the functions which the larger aquatic plants play in the aquatic complex". The "local reduction of wave action" (p. 307) is one of the factors mentioned. In Hyttödammen this is one of the conditions for the development of horizontal heterogeneity. Another condition is the presence of the two sources of incoming water, of different composition, i.e. the Dalälv and the springs. In the literature there are apparently no descriptions showing conditions similar to those of Hyttödammen. For lakes with broad littoral zones or rapidly encroaching vegetation or cut-off bays or lagoons, there is information about the development of horizontal heterogeneity for various environmental factors (e.g. PUKE 1949, GIEYSZTOR 1961, LOHAMMAR unpublished data on Lake Tåkern).

In Fig. 61, the ionic composition during the vegetation period is compared,

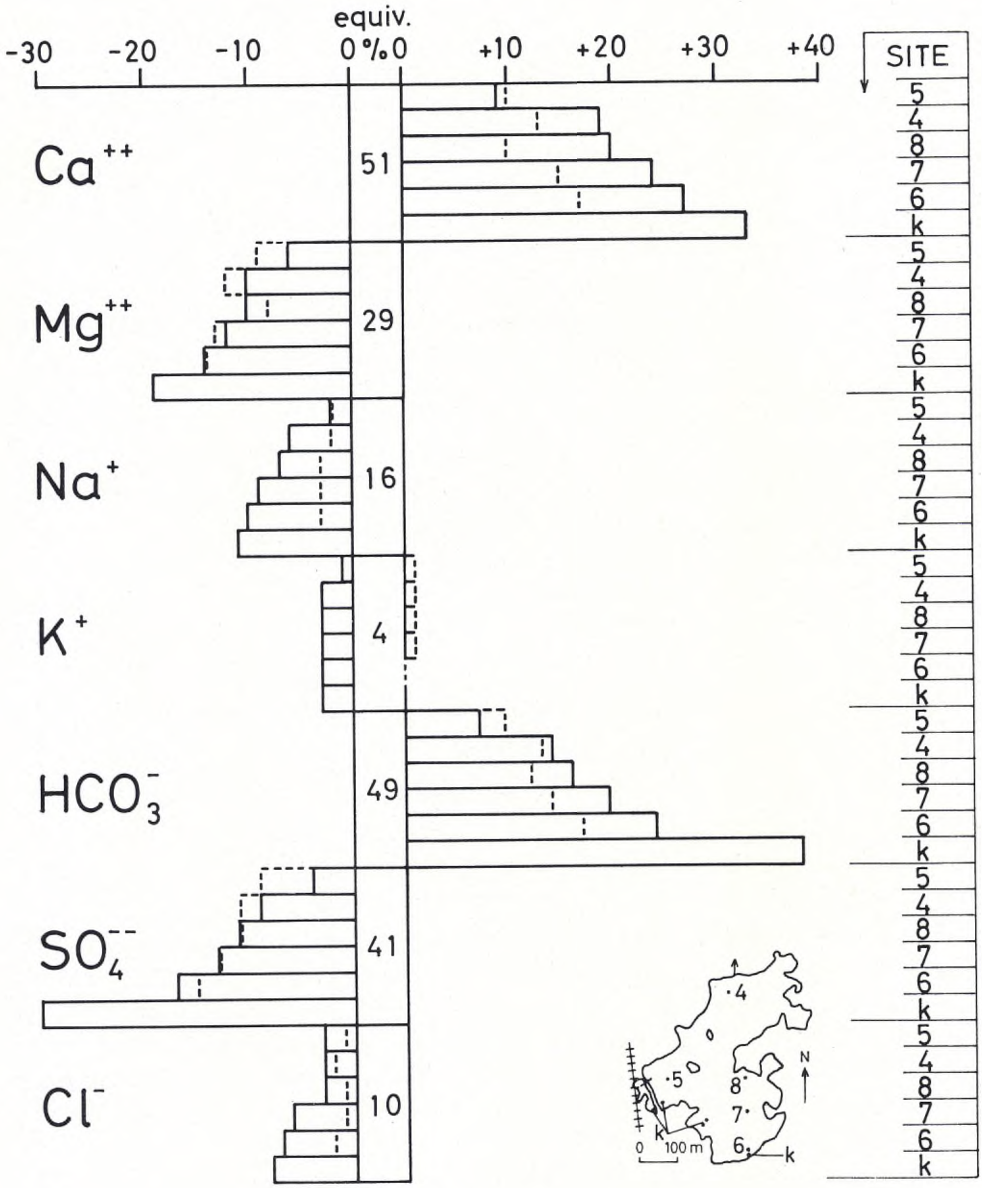


Fig. 61. The ionic composition of the pond water at different sites compared with that of the Daläly. The values at the sites are expressed as deviations from this base. The unbroken lines show the composition during the growing period of the higher vegetation and the dotted lines the composition after the dying down. Site k represents the mean of water taken from springs as indicated on the map.

for several different sites, with that after the vegetation has died down. The ionic composition of the spring water, as mean values, is also given there. These data have been compared with the ionic composition of the incoming Dalälv water. As an expression of the conditions during the vegetation period a mean value of the analysis data for Dalälv water and for the sites from the period June 18—Sept. 19 has been calculated. It is difficult to say exactly when *Sagittaria* begins to die down. It can, however, be seen that the leaves begin to wither at the end of August. Nevertheless the values from Sept. 19 have been included as part of the growth period. Dying down was not then complete since the stalks with fruits and remains of the leaves remained upright. Note also that the absolute values for the mobile ions, sodium, potassium and chloride, in Figs. 28—29 and 32—35 have already increased in the sampling on Aug. 27.

The ionic composition of Dalälv water has been used as a base and for each ion the sites and the spring water have been arranged in order of increasing deviation (positive or negative) from that base. With the exception of two magnesium, three chloride and five potassium values the order is the same. The least deviation from Dalälv water was observed at site 5; then followed sites 4, 8, 7, 6 and spring water. Thus site 4 is intermediate between Dalälv water and spring water, and the deviations in composition of the SE bay are explained by the influence of the spring water. For comparison between spring water and Dalälv water see p. 41.

In Fig. 61 the ionic composition after horizontal mixing has also been marked, by dotted lines. Even though it is not justified to compare values from a single analysis with a mean of 15 analyses at each site, it is possible to note some tendencies. The Figure shows that the mixing is not 100 % complete, but that significant changes take place in the direction of homogeneity of the water mass. In site 5 the calcium and bicarbonate proportions have increased in the direction of the composition of the spring water, whereas at other sites they have decreased. For magnesium and sulphate the changes were not so similar for the different sites. As observed above, (p. 61), this is due to their greater variation in the analysis material as a whole. For sodium, potassium and chloride quite good homogenization could be observed. However, it may be noted that after mixing these ions increase to contents which for all of them are higher than before mixing. This additional amount probably originates from the vegetation. (See Figs. 28—29 and 32—35 and explanation below.)

2. Mineral circulation

(a) *Chloride, sodium and potassium.*

The vegetation is known to have an effect on the ionic composition through ion uptake during the period of growth. The ions are taken up partly from the water and partly from the sediment. Uptake from the sediment by rooted vegetation can also affect the ionic composition of the water, since mobile ions (sodium, potassium and chloride) can move from the water to the sediment (see below, pp. 87—88). As has been mentioned above, (p. 6) during the summer a rapid decrease in the absolute content in the water of these easily mobile ions can be observed. This differs from observations which have been made for lakes. HÖLL (1951, p. 141) writes, for example, about potassium content of lake water: "Ein starkes Absinken des Kaliumgehalts habe ich weder bei normalen Seen noch bei solchen mit starker Phytoplanktonentwicklung gefunden. Niemals habe ich wie bei Phosphat und Stickstoff Nullwerte für Kalium oder weniger als 0.5 mg/l. K gefunden".

The ions taken up are incorporated in the structure of the cell or are accumulated in the cell sap. Different ions are concentrated to a different extent by different species, and the same species varies in uptake at different places. See, for example, SCHUETTE and HOFFMAN (1922), SCHUETTE and ALDER (1928 and 1929), LEHTORANTA (1956, p. 154) and FORSBERG (1960, p. 107 and Table 7). The degree of concentration also varies with the age of the plant. STENLID (1958) states, for land plants, that young parts have high contents. In older plants there is a movement from leaves to fruits. SOLSKI (1962) has shown for water plants (*Typha latifolia*) that the potassium content, in mg per g dry weight, is highest at the end of May. In addition, in his two investigation years the contents were approximately the same on the same date.

As early as 1908, LECLERC and BREAZEALE showed that minerals accumulate in plants, and may easily be leached out. They observed that hay may lose 50 % of its minerals if there is rain after it is cut. The laws governing the degree of uptake seem still to be unknown in detail. As an example of some of the pieces of the puzzle which have been described, GESSNER (1959, pp. 431—2), on the importance of potassium and sodium for cell physiology and on how the plant aims at a balance between them, may be referred to. When one ion is taken up, another is removed through ion antagonism.

According to the literature, the distribution of uptake ability between the various parts of a water plant covers a complete scale from plants which take up only through parts under water to those which are thought to take up only through the roots. LOHAMMAR (1938) summarizes "dass die Wurzelfesten Hydrophyten in ihrer Mehrzahl ihre Nährsalze hauptsächlich aus dem Boden beziehen". *Sagittaria* can also be grouped here, as it is rooted, and as it has a small leaf area. Plants with roots but with a large leaf area might perhaps take up the main part of their nutrients through the leaves. *Sagittaria longirostra*, according to TITCOMB (1924), has roots up to 60 cm long.

There is, however, another possible path for ions from water to plant, i.e. through direct uptake by floating leaves and perhaps also stalks. NÖMMIK (1962) refers to different experiments which have been done with land plants where various nutrient substances important for plants have been applied by leaf spraying and where positive results have been achieved.

Thus *Sagittaria* probably relies mainly on the bottom for its nutrient uptake. The bottom of Hyttödammen is rather different from that of a lake, for example. It is very young (25 years) judged on a lake time scale, so that no significant organic sediments have been formed. Nor does sediment formation go on normally, because every year Hyttödammen is drained of water, and a large part of the organic production is removed, partly as fish, partly as sediment in the water drained away. The bottom of Hyttödammen loses on drainage not only organic constituents but also easily soluble inorganic salts. The removal is mainly of potassium, sodium and chloride, and not, for example, calcium, as is apparent from the following data about the character of the sediment of Hyttödammen. (H below.) For comparison, values for some exchangeable cations from the sediment of the eutrophic Ösbysjön (Ö below) have been taken from AHL (1964). The figures are in mg/100 g air-dry soil. The analyses of the sediment of Hyttödammen have been made by Statens Lantbrukskemiska Kontrollanstalt.

Sediment layer	Ca		Na		K		Cl	
	H	Ö	H	Ö	H	Ö	H	Ö
0—5 cm	3,150	1,320	8.7	42.6	13.5	65.3	0.72	—
5—10 cm	4,560	1,300	9.1	41.4	6.0	64.5	0.75	—

The significance of leaching has been shown experimentally for chloride by Dr O. JOHANSSON, Uppsala, who found in agricultural research in pot and field experiments (supplement to the Minutes of the Soil Survey Committee at the Royal Agricultural College, Uppsala, § 9 March 9 1963) that after harvest and after leaching out by normal annual precipitation the soil contains 0 mg Cl/100 g air-dry soil. After fertilization with 2,400 kg KCl/ha there was 0 mg Cl/100 g air-dry soil in the layer 0—20 cm and 1—2 mg Cl/100 g air-dry soil in the layers below, down to a depth of 80 cm.

The contents of the readily soluble ions which are present in the bottom of Hyttödammen are probably not sufficient to meet the requirements of the aquatic vegetation. The only feasible explanation is that the vegetation takes up ions from the water, via the sediment, according to the hypothesis put forward on pp. 86—87 above. That the contents of other ions such as calcium and bicarbonate, which are quantitatively important for the growth of the cells, are not affected in the same way as sodium, potassium and chloride depends on different factors. As the values for exchangeable calcium ions show, the calcium content in the sediment of Hyttödammen is sufficiently high to meet the requirements of the vegetation and, besides, calcium is not so mobile that significant movement between water and sediment can take place. WILSON (1939) gives a survey of the literature in which the importance of the bottom for the higher aquatic plant vegetation is discussed.

According to EMANUELSSON *et al.* (1954) the fact that there is comparatively more calcium than sodium or chloride in the precipitation is of minor importance as an explanation of the unchanged calcium contents in the water. As calculated from their values, the Gävle area receives *c.* 8 kg calcium per hectar a year, *c.* 6 kg sodium and *c.* 3.5 kg chloride.

The ions transferred from water to vegetation, in the way mentioned above, move quite rapidly back to the water by diffusion when the vegetation dies down. For Hyttödammen it is not possible to demonstrate the probability of this explanation by measurements. There are no flow measurements for the incoming and outgoing water, and it is hardly possible to make such measurements for the springs. According to SOLSKI (1962) the maximum amount of calcium is released from dried vegetation (*Lemna gibba, Typha latifolia* and *Potamogeton lucens*) within 24 hours. For fresh vegetation the release is equally rapid if the vegetation is first broken up, but if it is not broken up it takes 3—4 days.

PENFOUND (1956) has shown that production is high for aquatic vegetation. *Typha latifolia* had the highest production in early June, 10.94 g C/m^2/day. ODUM (1954) gives 8.6 as a maximum value for *Sagittaria*. These figures are higher than those reported for production by land vegetation. They also suggest that the other trophic levels in Hyttödammen will not be able to contribute such a large quantity of the easily mobile ions, when they decrease in the autumn, as will the higher plants. FORSBERG (1960) showed that in Ösbysjön the ratio between the standing crop of *Chara*, which was dominant in the vegetation, and the maximum amount of phytoplankton, calculated as mg/m^2, was $1.7 \cdot 10^3$.

The nutrient-rich character of the aquatic vegetation has also been shown by animal husbandry. NELSON *et al.* (1939) reported growth experiments with rats which were fed on different aquatic vegetation to show the content of vitamins in the plants. Chemical and biochemical analysis data for some aquatic plants are also given. SEIDEL (1955) has also shown the nutrient-rich character of *Scirpus lacustris*.

Thus one can say that other authors have observed concentration of nutrients in the plants, and that uptake of these by *Sagittaria* occurs through the roots. In the conditions prevailing in Hyttödammen it has been shown that this uptake causes a decrease in the contents of the easily mobile ions in the water. It seems probable that *Sagittaria* takes up nutrients directly from the water and by means of the roots since there is a well-developed root system and the leaves are partly floating on the surface and partly stand above the water level.

(b) *Phosphorus.*

The role of phosphorus in mineral circulation in water has been the subject of many investigations, which have been reviewed by HUTCHINSON (1957). It is apparent that excess phosphorus is rapidly removed from the water and retained either in the sediment or in organisms. The higher aquatic vegetation is one of the groups of organisms which has been subjected to detailed study in respect to removal of phosphorus. BROCK and HOLDEN (1957) and HOLDEN (1959, 1961) consider, on the basis of fertilization experiments in Scottish freshwater lochs, that macrophytes and attached algae are most active in removing phosphorus from the water, with 20—70 %. They found that of those species dominant in the vegetation, no significant uptake occurred by *Lobelia dortmanna, Littorella uniflora, Nymphaea alba, Equisetum fluviatile* or *Carex rostrata.* However, for *Myriophyllum spicatum, Potamogeton praelongus, P. perfoliatus* and *P. gramineus* significant uptake was observed. These two groups of plants differing in phosphate uptake both have well-developed roots, but the second one has also a large leaf area for uptake (see above pp. 86—7). Any possible significance of these important differences of principle in the way in which nutrient substances are taken up by different plants does not seem to have been taken into consideration by BROOK and HOLDEN in drawing their conclusions.

In a summary of his earlier published results, HAYES (1962) points out the role of bacteria in delaying the passage of the phosphate to the sediment and thereby its removal. He has done aquarium experiments with radiophosphorus to show the relation of uptake by plants (*Eriocaulon, Utricularia* and *Sphagnum*) to uptake by bacteria. With only plants present, the phosphorus content of the water sinks rapidly, in agreement with BROOK's and HOLDEN's theory. If bacteria are added, the phosphorus content sinks slowly. "The effect of bacteria is to hold phosphorus in the water and prevent the large loss to the bottom plants. This is because bacteria hold large quantities of phosphorus in their cells and produce soluble organic radiophosphorus, which the plant presumably cannot assimilate" (p. 658). It seems that the high values of phosphate-P in Hyttödammen might be due to bacteria, according to HAYES. BROOK's and HOLDEN's theory seems to be correct if the type of vegetation which occurs is taken into account and if the content of bacteria is low.

To obtain a value for the bacteria content in water, samples were taken at sites 4, 5 and 6 on Aug. 26 1963 at a depth of 0.1 m. The laboratory work was done by Dr. V. TULLANDER of the Microbiological Institute, the Agricultural College, and gave the following values:

Sites:	4	5	6
Agar bacteria 24°/ml/3 days	2,500	22,000	6,900
Total number of bacteria in millions/ml	0.7	1.0	1.3

Even if the value of a single sample is only approximate it is clear that the agar bacteria content is many times higher than in unpolluted lakes in the surroundings of Uppsala (TULLANDER, 1962). The total content of bacteria determined with the membrane filter procedure shows that there may be most bacteria in those parts of the pond that have dense vegetation.

(c) *Silicon.*

The observed decrease in Figs. 57 and 58 in the pond for silicon is probably due mainly to uptake by the Aufwuchs. These algae are abundant, and have been investigated by Mr. L. KRONBORG. (Data will be published later.) Other organisms that might influence the content of silicon in water are the diatoms in the phytoplankton, and higher aquatic vegetation. The increase in diatoms in the phytoplankton has been related to decrease in silicon content (for example, WILLÉN 1959 for Görväln). However, the diatoms are sparse in Hyttödammen, according to the determinations of the standing crop of phytoplankton made by Dr. A. NAUWERCK, Uppsala in connection with my investigations of the primary production. For the higher aquatic vegetation, it has been shown that silicon is a constituent of plant organs (for example by SCHUETTE and HOFFMAN 1922, SCHUETTE and ALDER 1928, 1929, and FORSBERG 1960). The higher vegetation in Hyttödammen probably takes up silicon through the roots. Silicon cannot easily move through the sediment and thus the higher vegetation cannot cause a decrease in the silicon content of the water.

VII. Summary

In this article an account is given of the physical and chemical conditions in Hyttödammen. Hyttödammen has an area of *c.* 12 ha and an average depth of *c.* 1 m. It is used for rearing of first-summer, or one-year-old salmon. The pond receives water mainly from the river Dalälv via a flume, but some springs opening into the pond also contribute. The Dalälv and spring water have quite different chemical properties. For example, the specific conductivity of the spring water is *c.* $250 \cdot 10^{-6}$, whereas that of Dalälv water is *c.* $30—40 \cdot 10^{-6}$. The spring water is relatively richer in calcium and bicarbonate, in comparison with Dalälv water and standard composition.

The abundant vegetation, mainly *Sagittaria sagittifolia* L., has a great effect. Firstly, horizontal heterogeneity can build up, partly because of the influence of spring water; secondly, the most mobile ions (potassium, sodium and chloride) are taken up from the water. Because of leaching out of the sediment each year, in connection with draining the pond and removing the fish, the contents of these ions in the sediment are so low that *Sagittaria*'s requirement for them cannot thereby be met. The remaining amounts are taken from the water, and during the vegetation period this causes move-

ment from the water to the sediment. *Sagittaria* takes up the greater part of its nutrients through the roots. When the vegetation dies down the ions which have been taken up are released into the water.

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The bacteria analysis was by Dr. V. TULLANDER.

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Studies on the bottom fauna of impounded lakes in southern Norway

(Tunnhovdfjord, Paalsbufjord and Rödungen)

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Contents

1. The lakes

The Norwegian lake Tunnhovdfjord, situated in the upper part of Numedalslaagen at an altitude of 735 metres, serves as a water-storage basin for power generation. Since 1919 the level of the water has been raised by 18 metres in relation to the previous low-water level. The rhythm of the annual fluctuations of the water level corresponds to that of other impounded lakes in the Scandinavian high mountains. This means a high and relatively stationary water level during the summer. The stored water is used in the course of the winter until low water is reached in the spring.

The drowned area consists of forest upon rocky ground with mosses and heather. Prior to the damming-up the big conifers had been felled, but the stumps, minor trees, shrubs, and rubbish were left.

Similar conditions apply to Lake Paalsbufjord, situated immediately above Tunnhovdfjord at an altitude of 750 metres. Its annual amplitude is 23.5 metres.

Lake Rödungen, at an altitude of 944 metres and with a fluctuation of the water level amounting to 6.5 metres, is fed from a limited drainage area. For this reason several years are required for its being filled.

2. Earlier investigations

With the intention of elucidating the effect of the regulation primarily upon the fish fauna of the lakes, investigations have been carried out since the time before the impoundment (DAHL 1926, 1931). The investigations of

DAHL in the years 1917, 1920 and 1923 include among other things the bottom fauna in Lake Tunnhovdfjord. DAHL established that the regulation resulted in a reduction of numerous organisms that normally occupied the littoral region of the lake. Animals important as fish food, such as *Gammarus,* larvae of *Sialis, Trichoptera* and *Ephemeroptera,* seemed to be eliminated, and the gastropods had become scarcer. On the other hand there occurred a decided flourishing of the small benthonic crustaceans, e.g. *Eurycercus lamellatus* MÜLL. and *Sida crystallina* MÜLL. as well as of the pelagic forms, e.g. *Holopedium gibberum* ZADD. and *Daphnia longispina* MÜLL.

Investigations carried out ten years after the regulation by HUITFELDT-KAAS (1935) revealed in the lake a fauna richer in insects, coupled with a decline of the small crustaceans. This shows that the flourishing of, e.g., benthonic cladocerans is of short duration.

The detailed investigations into the fish fauna in the lake carried out in more recent years show the large insect larvae form an important item in the diet of the fish (AASS, personal communication). The observations indicate that these larvae are more resistant to the regulated conditions of the lake than are other typical fish food organisms (AASS 1957).

Bottom samples and stomach contents of brown trout, *Salmo trutta* L., obtained by AASS in 1960—61 proved to contain *Siphlonurus lacustris* EAT. and a few isolated specimens of *Heptagenia fuscogrisea* RETZ. *Siphlonurus lacustris* also occurs in other impounded waters, e.g. in Lake Blåsjön in northern Sweden (GRIMÅS 1961) and in Lake Arnensee in the Swiss Alps (GRIMÅS and NILSSON 1962). This ephemerid belongs to the few bigger insects that can be expected to take possession of the regulation zone in this type of impounded lake.

3. The investigation 1961

Lake Tunnhovdfjord and the neighbouring impounded lakes Paalsbufjord and Rödungen were studied in October 1961.

The physico-chemical properties of the water are presented in Table 1. The lakes can be characterized as oligotrophic lakes with clear water. The relatively high values for transparency prove the absence of any considerable turbidity resulting from the regulation. Most of the loose sediments of the regulated zones ought to have been transported to areas below the draw-down limit.

Great parts of the drained area of Lake Tunnhovdfjord are covered by remains of the former forest, especially by stumps of trees, and limited areas with the former moss carpet are also found in more exposed parts of the lake. With the exception of less exposed areas, e.g. the north-western bay of the lake and Bergevika, where fine sediments occur as high as the shoreline,

Table 1. Physico-chemical data on October 14, 1961.

	Tunnhovdfjord	Paalsbufjord	Rödungen
Transparency, m.	10.6	7.7	—
Surface temperature, C	9.3	8.8	7.2
pH	6.8	6.9	6.9
$H_{20} \cdot 10^6$	18.6	18.1	20.1
HCO_3 μequ/l	88	88	121
SO_4 ,,	67	61	57
Cl ,,	13	14	13
Ca ,,	112	90	152
Mg ,,	28	46	4
Na ,,	22	22	22
K ,,	4	6	9
Tot N μg/l	86	64	66
Tot P ,,	3.8	2.9	4.2
PO_4 ,,	0.3	0.2	0.6

(The chemical analyses were made by Dr. T. AHL at the Limnological Institute of the University of Uppsala)

the sediments consist of sand, gravel and blocks. The organogenic material of the profundal contains a considerable proportion of coarse detritus derived from the forests, e.g. conifer needles, strands of roots, fragments of bark and conifer cones.

The fauna

The examination of the bottom in Tunnhovdfjord comprise both exposed and more sheltered littoral areas down to the profundal region below the draw-down limit. In Paalsbufjord the littoral fauna and in Rödungen the shore fauna have been studied.

The investigation is directed mainly towards the qualitative composition of the bottom fauna, but has been supplemented by quantitative material from Tunnhovdfjord.

Insects. One of the most important results is the establishment of the bigger insect larvae in the littoral of Tunnhovdfjord to an extent that differs from that in other impounded lakes examined. Within exposed areas these insects seem to be concentrated mainly in the stumps still fixed in the ground. These contain a considerable quantity of larvae of plecopters, ephemerids and trichopters (Table 2.). The larvae are also found in the loose rubbish which drifts along the shores. The plecopter *Nemoura cinerea* likewise occurs spread over the naked rocky bottoms of the area. In sheltered bays the distribution of the animals over the bottom sediments is more uniform. Among the larger species *Siphlonurus lacustris* is the dominant form with, in addition, semiterrestrial larvae of dolichopodids and tipulids.

As in other regulated lakes, the concentration of bottom animals is higher in the immediate vicinity of feeders, where the fauna also receives contribu-

Table 2. Bigger insect larvae established in the littoral of Lake Tunnhovdfjord.

Exposed bottoms		Sheltered bays
Block bottoms:	*Nemoura cinerea* RETZ.	*Nemoura cinerea* RETZ. *Siphlonurus lacustris* EAT. *Leptophlebia marginata* L. *Baëtis* sp. *Adelphomyia* sp. *Dolichopodidae*
Stumps of trees:	*Nemoura cinerea* RETZ. *Siphlonurus lacustris* EAT. *Leptophlebia marginata* L. *Limnophilus bipunctatus* CURT. *Phryganea obsoleta* HAG.	

tions of rheophile forms, e.g. *Baëtis rhodani* PICT., *Heptagenia sulphurea* MÜLL., *Diura nanseni* KEMP., *Polycentropus flavomaculatus* PICT. and *Rhyacophila nubila* ZETT.

The experiences gained in Paalsbufjord suggest that the conditions in the littoral of this lake agree on the whole with those in Tunnhovdfjord. On the occasion of the sampling the upper littoral appeared poorer, but this is probably connected with the circumstance that the lake had only recently been filled.

The greatest divergences from the customary picture of regulation were observed in Lake Rödungen. Here the shore fauna seemed to have been very little affected by the regulation, and larvae of ephemerids, plecopters, trichopters and dytiscids occurred abundantly along the shores together with *Gammarus*. Common were for instance larvae of *Leptophlebia marginata*, *Nemoura picteti* KLAP. and *Capnia atra* MORT. but also imagines of *Haliplus fulvus* FABR., *Hydroporus palustris* L. and *Callicorixa concinna* FIEB. The latest lowering of the water level took place in 1959, and it appears probable that the slow rhythm of regulation, in combination with a limited amplitude of the water, creates in Lake Rödungen conditions which are more favourable to the fauna than those obtaining in the impounded lakes situated nearby.

A long-term effect of the regulation means in most of the studied lakes a change in the balance within the fauna to the advantage of the chironomids (RAWSON 1958, GRIMÅS 1962, AASS 1963). It can be assumed that this development also applies to Lake Tunnhovdfjord. The data obtained by DAHL in 1917 do not include exact information about the number of the minor crustaceans, but the share of the chironomids in the total fauna can be estimated at less than 24 per cent. In the winter of 1927 the corresponding figure in Paalsbufjord was 37 per cent. In samples from Tunnhovdfjord from 1961 the larvae of dipters predominate numerically in the fauna, and in the quantitative material constitute 52 per cent of the animals.

The proportion of semiterrestrial larvae of dipters is great in the upper littoral both in exposed and in more sheltered regions, the genera *Pseudo-*

smittia and *Stilobezzia,* for instance, occupying a dominant position together with *Psectrocladius* and *Tanytarsus.*

The largest number of chironomid species appears somewhat lower down in the littoral within sheltered regions with an uninterrupted cover of sediments. Within the depth zone 5—6 metres we may mention representatives of the genera *Psectrocladius, Sergentia, Tanytarsus, Procladius, Ablabesmyia, Polypedilum* and *Cricotopus* and, less frequent, *Protanypus, Constempellina, Microtendipes, Chironomus, Demicryptochironomus* and the ceratopogonid *Stilobezzia.* In more exposed environments within the same depth zone the chironomid fauna is, however, poor and larvae of tanypodines are encountered mainly in bottoms with old moss vegetation. The *Tanytarsus gregarius*-group and *Orthocladius naumanni* BRUNDIN also occur within the region.

Towards the deeper parts of the littoral (depth zone 10—12 metres) the larvae of tanypodines are still common, but here loose sediments and mosses occur more frequently and with them also other species within the genera *Heterotrissocladius, Trissocladius, Tanytarsus, Microspectra* and *Microtendipes.*

The chironomid fauna of the profundal (depth 25 metres) consists mainly of species from the main group *Chironomini,* particularly *Stichtochironomus,* but also *Microtendipes, Polypedilum* and *Sergentia.* In addition there occur *Microspectra, Constempellina, Stempellinella, Cricotopus* and *Procladius.*

In giving a general summary of the chironomid fauna we can establish that orthocladines and tanytarsines occupy a very marked position in the littoral fauna of the lake, and that they are the only forms encountered in its upper parts. A richer assortment of species with, *inter alia,* representatives of the *Chironomini* can be encountered only in littoral bottoms that are sheltered from erosion and covered by uninterrupted layers of fine sediments. *Stichtochironomus rosenschöldi* EDW. is restricted to profundal areas below the draw-down limit, a fact which might be interpreted as a result of the regulation. This species is characteristic of many lakes in the Scandinavian high mountains, where it normally also occupies the littoral (LENZ 1928, BRUNDIN 1949).

Other bottom animals. Of the other larger bottom animals which previously occurred in the littoral of Lake Tunnhovdfjord only a small remnant is left. *Lymnea peregra* MÜLL. has been encountered in isolated individuals in the sheltered bays, and *Asellus aquaticus* L. in the neighbourhood of the draw-down limit. An isolated find of *Gammarus* in the stomach of a brown trout may also be mentioned (AASS, personal communication), but the occurrence in the lake of this once so important prey cannot be taken for granted. AASS also reports the presence of *Lepidurus* in the lake after the impoundment.

In Tunnhovdfjord the cladocers reach their maximum development at the beginning of September (DAHL 1931). This explains in part the relatively

Table 3. Estimated quantity of bottom animals in the Lake Tunnhovdfjord, 1961. Individuals/sq.m and gramme/sq.m (in italics).

Depth zone	Sheltered bays		Exposed bottoms			
			bare sediments		sediments+ moss cover	
0— 1 m	5,280	*3.2*	249	*0.1*	—	—
5— 6 m	660	*0.7*	264	*0.2*	748	*1.3*
10—11 m	—	—	594	*0.6*	—	—
25—26 m	—	—	1.870	*2.4*	—	—

small proportion, 9 per cent, the total fauna of the lake represented by them at the time of the present investigation (middle of October). In the bottoms that are normally influenced by regulation *Simocephalus vetulus* Müll. occurs down to regions below the draw-down limit together with isolated specimens of *Daphnia longispina* and *Holopedium gibberum*. In the sheltered bays the cladocer fauna is considerably richer and *Ophryoxus gracilis* Sars., *Eurycercus lamellatus* and *Alona quadrangularis* Müll. are common up to the shoreline. *Sida crystallina,* characterized by Dahl as very common, could not be traced in the lake (cf. Huitfeldt-Kaas 1935).

Next to the chironomids the oligochaets contain the greatest number of individuals and constitute 31 per cent of the material. Like many other groups of animals the oligochaet fauna is best developed in the sheltered bays. In the normally eroded bottoms of the drainage area the oligochaets are rare and occur mainly in connection with the old moss carpet. As in other impounded lakes examined, enchytreids occur in a narrow zone in the upper littoral, while the naidids dominate in the sediments of the profundal.

The pisidids are rare above the draw-down limit, but have been encountered in the north-western bay of the lake up to the middle littoral.

Among the remaining organisms we may mention hydras along block-strewn shores and nematods with a distribution that agrees on the whole with that of the oligochaetes.

Quantity. The quantitative material has been collected by means of a bottom sampler of the type Ekman-Birge and thus covers only regions with loose sediments. Sifting was performed through 0.6 mm mesh, and the weighing was carried out of preserved material to a limit of ±0.1 mg. The material does not include enchytreids and nematodes, the small size of which is assumed to cause losses in the sifting.

The size of the material (15 bottom samples) does not permit more detailed analyses, but should give a rough picture of the conditions in Tunnhovdfjord.

The results (Table 3) agree with the experiences from other impounded lakes examined. The greater part of the dammed-up region is poor in individuals, and the bathymetrical distribution of the animals shows, contrary to what is found in normal lakes, an inverted course with maximum abundance below the draw-down limit, in this case in the profundal.

Different conditions arise in areas that are protected from erosion and covered by a continuous layer of fine sediments. This permits a distribution similar to the natural one, with maximum abundance within the littoral. Scattered, limited portions of the former moss cover also house a fauna which is richer in individuals than the eroded minerogene bottoms, and the remaining tree stumps in the drainage area constitute similar refuges for a more abundant fauna.

4. Discussion

Earlier examinations of the bottom fauna in impounded lakes in the Scandinavian high mountains have shown that the annual drying up and freezing of the bottoms in the zone of regulation, together with the changed composition of the bottom sediments of the lakes, is of great importance for the qualitative composition of the fauna. In certain circumstances the spectrum of species can, however, be surprisingly broad and the biomass of the remaining fauna can be high with regard to the extreme conditions prevailing within the regulated region during the winter. A modifying factor seems to be the availability of fairly undifferentiated organogenic material in different stages of decomposition. In bottom areas which are exposed to freezing in winter, and in which detritus is the only source of food, an abundance of up to 8,000 animals/m^2 has been established. Here we find, among insects and crustaceans, species, which normally dwell in the parts of the lake that contain vegetation but have been eliminated from the eroded regulation zones (GRIMÅS 1960, 1962).

In Tunnhovdsfjord the conditions are similar. The eroded minerogene bottoms, dominating the drainage zone, contain a fauna poor in species and individuals. The data about the quantity by weight of bottom animals in the littoral of the lake in 1917 vary between 0.6 and 2.8 g/m^2 (DAHL 1926). In 1961 these values lay between 0.1 and 1.3 g/m^2 for the bottoms normally influenced by the regulation. In spite of the long period of regulation, there nevertheless occur in the littoral areas exhibiting a modified effect of the regulation. The importance for the production of fish of such areas which serve as refuges for a richer fauna is not exactly known at present, but can be traced in the choice of food shown by the fish (NILSSON 1961). Their importance is, of course, to be connected with their size, but also to the specific composition of their fauna, e.g. the availability of their organisms as fish food (cf. GRIMÅS 1963).

The major part of the fauna of the sheltered bays is embedded in the sediments and for this reason probably less accessible as food for brown trout and char, *Salvelinus alpinus* L., in Tunnhovdfjord. But there exists in these areas as tendency to retain also more available organisms like gastropods, the larger insect larvae and benthonic cladocerans which in higher concentrations can be of importance as objects of prey, e.g. *Siphlonurus lacustris.*

The fauna of the limited "moss islands" is dominated by oligochaetes which can be utilized as food by the actual fishes only to a very small extent.

The main feature distinguishing Tunnhovdfjord from other regulated lakes examined is the occurrence of the former vegetation of trees and shrubs in the damming-up zone.

The decisive rôle of the microflora by the decomposition of cellulose has been established (cf. OVERGAARD-NIELSEN 1962). It is of interest that in the bottoms of Tunnhovdfjord the larvae of many aquatic insects seem to be able to exploit these sources in the form of wood, either by symbiosis with microorganisms or by the intercalation of several links in the trophic chain. Among aquatic organisms *Gammarus pulex* DE GEER has previously been observed to feed on cellulose in the form of paper (HEITKØTTER 1963).

There are many factors suggesting that the insect fauna in the drowned forest vegetation in Tunnhovdfjord is of importance for the fish fauna. The remains of the woody vegetation still fixed in the ground occur in relatively uniform distribution over great portions of the drainage zone and cover a considerable percentage of the total area. The fauna consists of organisms which normally form part of the main food of the fishes. The mobile larvae are concentrated in the remains of the vegetation and some of them are also spread over neighbouring bottoms. Their mobility, size and the type of aggregation (cf. IVLEV, 1961) enhance the availability of the larvae as prey and the insects are also available during periods of emergence and oviposition. The study of the large material of fishes collected in the lake since 1949 has not been definitely concluded, but random samples chosen among the material from recent years reveal stomachs of brown trout filled exclusively with the bigger larvae of insects, e.g. *Siphlonurus, Limnophilus* and *Phryganea* (AASS, personal communication). At present the char forms the main food of the larger brown trout in Tunnhovdfjord (AASS 1961). It seems possible that the availability of bigger insects in the bottom fauna of the lake contributes to a faster growth of this fraction of the brown trout population and facilitates the transition to feeding on fish.

During the first years of the regulation DAHL found in Tunnhovdfjord a fauna which was very poor with the exception of the small crustaceans. Particularly remarkable is the reduction in the case of the insects, the bigger forms of which are altoghether absent in material from the bottoms and the stomachs of fishes. The observations made by HUITFELDT-KAAS after ten years of regulation provide an entirely different picture. The flourishing of the small crustaceans has come to an end, and the insects, represented also by bigger forms such as ephemerids, trichopters and dytiscids, form a considerable percentage of the material.

As a short-term effect immediate changes in the bottom fauna can be expected after different kinds of interference, both after the drowning of new areas and a lowering of the surface of the water. NILSSON (1963) reports a temporary, but strong drop in abundance as an immediate result of the regulation of Lake Ransaren. Such changes have also been proved in connection with a widening of the amplitude of regulation in an old regulated lake (GRIMÅS 1962).

Changes in the specific balance within the fauna in the course of such a phase in the regulation history of a lake might be correlated with mechanical interference with the environment of the bottom fauna. New sediments are exposed to erosion by the increased amplitude of the water, and a process of redisposition, involving the transport of loose sediments to regions below the draw down limit, is accentuated. Thus the first years of the regulation bring about very unstable conditions in the sediment cover of the bottoms which affect not only the regulated zone but also deeper regions that are overlain by the eroded material.

The greatest sensitivity to these disturbances is probably found in those bottom animals which dwell within the zone of contact between water and sediment, e.g. a large part of the insect fauna. The small crustaceans that are found close to the bottoms are on the other hand favoured, owing probably to the fact that more food in the form of small particles of detritus or bacteria is made accessible.

The leaching-out of the zone of regulation brings about a stabilization of conditions in the bottoms, and a fauna that is richer in species is re-established. The environmental conditions for the fauna are, however, changed, and the annually recurring extreme conditions of the winter influence the specific composition of the fauna. Characteristic are the dominance of orthocladiines and tanytarsines in the chironomid fauna of the regulated zone in Tunnhovdfjord, and also the proportion of semi-terrestrial larvae in the littoral of the lake.

In the course of the subsequent period of regulation the supply of organogenic material is of decisive influence upon the biomass of animals in the bottoms. A slow deterioration of the conditions can be assumed, down to the level where allochtonous material from the neighbourhood and products of the plankton production of the lake become decisive.

Conditions in Lake Tunnhovdfjord show that material relatively difficult of access can be utilized as a food basis by many organisms. In spite of the long period of regulation, 45 years, considerable quantities of utilizable material remain within the damming-up area in the shape of the original forest vegetation which is capable of preserving in the lake organisms that are important as fish food.

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5. Summary

1. The qualitative composition of the bottom fauna was studied in the impounded subarctic Lakes Tunnhovdfjord, Paalsbufjord and Rödungen in southern Norway. The investigation is supplemented by quantitative material from Tunnhovdfjord.

2. Within the regulated zone, regions with a greater abundance, so-called refuges, were shown to exist in Tunnhovdfjord. Their importance as feeding grounds for fish is discussed.

3. The specific composition of the fauna in the lakes exhibits deviations from the hitherto known picture of regulations.

4. In spite of a wide amplitude of the water-level fluctuation the occurrence of the larger insect larvae is considerable in the Lakes Tunnhovdfjord and Paalsbufjord. This is assumed to be due to the availability of organogenic material in the shape of drowned forest vegetation in the damming-up zones of the lakes. The wealth of the shore fauna in Lake Rödungen is attributed to the slow rhythm of regulation in the lake in combination with the restricted amplitude of the water.

5. The short- and long-term effects of the regulation upon the bottom fauna are discussed.

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Internal tagging of salmon smolts III

Final report on taggings 1952—55 and comments on the smolt production of a salmon river

By Arne Lindroth

I. Introduction

In the years 1952—55 close on 20,000 salmon smolts were tagged with internal tags and liberated in the Swedish river Indalsälven. The tagging technique, method of recapture, and returns for 1954 have been reported earlier (Lindroth 1953, 1955).

The introduction of an internal tag for Atlantic salmon smolt in the Baltic was intended to serve a dual purpose: to test the commonly used external tag developed by Carlin, and to aid in the estimation of the annual smolt output from the Baltic salmon rivers. Later Swedish tagging results have shown a strong influence of ecological factors upon tagging returns and, as the internal tagging experiments were not carried out with the use of the same stock of parr externally tagged as control, reliable comparisons are not possible. In spite of this failure, it seems justifiable to give a final report on the internal tagging experiments so far not repeated.

II. Experiments and returns

Table 1 gives the tagging experiments and pertaining returns in the home river by means of X-ray examination. The accidental returns made by commercial fishermen are specified in Table 2.

III. Discussion

It would be possible to discuss several details in salmon biology on hand the tagging results. As, however, the material collected by the Salmon Research Institute (formerly Migratory Fish Committee), comprising up to the end of 1962 750,000 salmon smolts tagged, forms a far better basis for future discussions, in the present connection mention will be made of only a few questions contributing to the main discussion of smolt output.

Experiments 1953: 1 a and b were intended to study the loss in the turbines of the Hölle power station. Returns from liberations above the power station, 1 a, proved in fact to be slightly higher. Turbine mortality may thus be neglected for the purposes of the present discussion.

Table 1. Internal tagging experiments 1952—55.

Expt.	Int. tag type	Ext. tag	Fish from	Date and place of liberation	Dist. fr. mouth, km	No.	Returns at Bergeforsen						Other returns			
							at sea age				total		river, smolt		sea or river large fish	
							·1+	·2	·3	·4	No.	%	by int. tag	by ext. tag	by int. tag	by ext. tag
1952: 6a[1]	A, B[2]	—	troughs	Sept., coast outside river	—	858	—	—	—	—	—	0	—	—	2	—
b[1]	A, B[2]	+	,,	Sept., coast outside river	—	255	—	—	—	—	—	0	—	—	1	3
						1,113	—	—	—	—	—	0				
8a	A	—	,,	Sept. 22, river	50	1,739	10	5	4	—	19	1.15	—	—	3	—
b	A	—	,,	Oct. 7, river	65	1,611	12	9	5	—	26	1.62	1	—	1	—
						3,350	22	14	9	—	45	1.3				
10	B[2]	—	large pond	Oct., river	25	2,250	20	5	4	—	29	1.3	1	—	—	—
1953: 1a	C	—	troughs	May 8—15, river above turbines	80	2,647	15	5	7	1	28	1,06	—	—	4	—
b	C	—	,,	May 8—15, river below turbines	80	2,645	16	9	5	—	30	1.14	—	—	3	—
c	C	—	,,	May 18, river	79	2,815	14	7	11	—	32	1.14	—	—	2	—
d	C	—	,,	May 19, river	10	832	2	2	2	—	6	0.72	—	—	1	—
e	C	+	,,	,, ,, ,,	10	582	—	1	1	—	2	0.34	—	—	(—)	49
						9,521	47	24	26	1	98	1.0				
7a	B[2]	—	ponds	Oct., river	2	789	—	—	—	—	—	0	—	—	—	—
b	B[2]	+	,,	,, ,,	2	411	—	—	—	—	—	0	(—)	7	—	4
						1,200	—	—	—	—	—	0	—	—	—	—
8	B[2]	—	large pond	Sept., river	2	174	—	—	—	—	—	0	—	—	—	—
1954: 1	A, C	—	wild smolt	June, river	2	80	—	2	—	—	2	2.5	—	—	—	—
4	C	—	pond, trough	June 28, river	50	759	1	—	—	—	1	0.1	8	—	—	—
16[3]	C	—	ponds	Dec., river	10	898	—	—	—	—	—	0	—	—	—	—
18[3]	C	—	,,	1955 spring, river	10	519	—	—	—	—	—	0	—	—	—	—
Total						19,864	90	45	39	1	175	0.88	10	—	17	—

[1] Parr not in good condition, dermal inflammations common, therefore liberated not in river but off the coast.

[2] Tag type B unsuccessful. See LINDROTH 1955.

[3] These fish suffered from gas-bubble disease and may not have survived after liberation.

Table 2. Accidental returns of internal tags.

Expt.	Date	Length cm	Place
1952: 6 a	Jan. 1954	—	Baltic Sea (Gotland) in small salmon
	Spring 1954	—	Baltic Sea (Bight of Gdansk)
6 b	Jan. 1954	—	Baltic Sea (Gotland), in cod, external tag not found
8 a	Sept. 1954	48	Lower part of river on rod
	Sept. 1955	75	Sundsvall bay
	Dec. 1956	100	Baltic Sea (off Häradsskär)
8 b	April 1953	10.5	River, 50 km fr. mouth, electrofishing
	Aug. 1954	—	Sundsvall bay, bag net
1952: 10	June 1953	—	Lower part of river, angle
1953: 1 a	Dec. 1953	35	Baltic Sea (Gotland), hook
	Aug. 1954	(1.3 kg)	Sundsvall bay
	Sept. 1954	45	River Ume älv, 300 km to the north
	Dec. 1954	—	Baltic Sea (off county of Södermanland)
1 b	July 1954	70	North of Sundsvall bay
	Aug. 1954	(1.2 kg)	Sundsvall bay
	July 1956	—	Sundsvall bay, bag net
1 c	Okt. 1954	—	Off county of Stockholm
	July 1955	(4.4 kg)	Sundsvall bay
1 d	July 1954	52	Sundsvall bay
1954: 4	July 1954	—	Lower part of river, 7 ind. in smolt trap
	July 1954	—	River, 20 km from mouth, in stomach of merganser duckling

The recaptures were made in the fishing installations of Bergeforsen's power station 10 km from the river mouth, either in the gallery and trap over the tail-race tunnels of the station, or at a seine-net site 600 m downstream. We have now some indications that planted smolts have no urge to ascend their home river beyond the point of liberation. Planting in the river mouth may be suspected of giving inferior returns. The present material might corroborate this hypothesis. Experiment 1953: 1 contains groups of the same origin liberated at different places along the river. If groups a—c, liberated about 80 km upstream, are combined and compared with group d, liberated at the seine-net site, there is a difference in the percentage return, 1.11 as against 0.72. It seems wise to discard the groups where liberations have been made in the lower reaches.

The time of liberation is important (according to tagging results by the Salmon Research Institute). Mid-May to mid-June seems to give the best returns and appears to correspond to the period of natural smolt migration to the sea in this river.

The considerations stated above lead to the elimination of some of the experiments. The following remain to be discussed.

1952: 8 a and b. Hatchery, 2-summer-old parr from troughs, mean length 11.9 cm. Liberated Sept. 22 and Oct. 7 on rearing grounds in the river 50 and 65 km from the estuary. The parr must have wintered in the river and migrated to the sea with the wild smolt. They may have grown in the autumn after planting and probably in the spring also and have suffered an unknown winter loss in the river before migrating to the sea in the spring or early summer. Compared with hatchery smolt liberated in the spring, the return figures for these lots are too small on account of the winter loss and could be too large to the extent that wild smolts are superior to hatchery parr.

1952: 10. Hatchery 2-summer parr reared without artificial feeding in drainable lake during the second summer, mean length 14.8 cm. Liberated Oct. 10—13 on rearing ground 25 km from the estuary. The tag used was of poor quality (see LINDROTH 1955) and is likely to have killed some fish; in half of the returning 20 grilse the tag was recovered from the swimbladder, this position not being encountered in any of the 9 older fish. The errors in the return figures are the same as for the lots 1952: 8; moreover, the mean fish size in this lot was probably above average at sea migration, tending to give better survival.

1953: 1 a—c. These 3 lots consisted of hatchery 2-year parr, 13.4 cm mean length, of ordinary hatchery quality and liberated May 8—19 in the river 79—80 km upstream from estuary. This planting diverges from the recent smolt planting technique inasmuch as the fish were somewhat smaller.

To sum up, of the 13,707 fish liberated in the experiments considered, 8,107 (i.e. 1953: 1) are regarded as representative of — or at least not better than — smolts now liberated on a large scale. The remaining 5,600 fish have been planted under differing conditions. There is, however, in all no clear reason to regard them as superior to the other fish, and as the errors in representativity are difficult to evaluate no correction has been attempted. Overall return percentages are as follows:

Expt	No.	Returns at the sea age				
		· 1 +	· 2	· 3	· 4	combined[1]
1952: 8	3,350	0.65	0.42	0.27	—	1.34 ± 0.39
10	2,250	0.89	0.22	0.18	—	1.29 ± 0.47
1953: 1	8,107	0.56	0.26	0.28	0.01	1.11 ± 0.23
combined ..	13,707	6.63	0.29	0.26	0.01	1.20 ± 0.18

[1] 95 % confidence interval.

The confidence of the return figures is not all to bad.

For the computation of smolt output the percentage return has to be applied to some catch figure. The total catch of the river is composed of the catches of the power company, mentioned above, and commercial gear. The catching effort has varied through the years in question, 1954—57, and the catch statistics are not beyond doubt. Furthermore, a computation by means of total river catch would imply adjustment of tag returns to a higher catch level, and, as grilse are not caught or not always recorded as salmon in the commercial fishery, would mean ignoring the recovered grilse.

If total catch provides no appropriate reference figures, the experimental catch, X-ray examined for tags, is known. In 1954 1,570 grilse were examined and in 1955 890 small salmon of 2 years sea age. The numbers are not exact, as the aging has been performed on hand length-frequency curves. They could be used for the two younger age groups, however, but not for older fish. It is doubtful whether scale reading of some thousands of fish would have given more reliable figures. (See Addendum.)

Combining the experiments (and leaving aside 3 fish recovered 1955 which seem to have stayed in the river for an extra year after planting and migrated in 1954) we arrive at the following computation for the smolt year 1953:

Catch year	Planted tagged smolt	Percentage recovered [1]	No. examined	Total smolt output
1954	13,707	0.63 ± 0.13	1,570	250,000
1955	13,707	0.27 ± 0.09	890	330,000
combined	13.707	0.90 ± 0.16	2,460	270,000
combined excl. expt. 1952: 10	11,457	0.87 ± 0.17	2,460	280,000

[1] 95 % confidence interval.

The results indicate that the smolt output from the Indalsälven in 1953 had a magnitude of roughly 300,000. This statement postulates that the smolts used were representative of migrating smolts as to quality, migrating time, and so on. Certainly differences exist; on average they favour the wild smolt, and it would be wise to emphasize that the number given above is expressed in terms of hatchery smolts of the quality produced in Swedish hatcheries as far back as 1952—53.

A few tests of the results are possible.

a. The smolt output in 1953, say 280,000 (see above) comprised a lot of about 50,000 hatchery smolts. The number of wild smolts would then be about 230,000 produced on the nursery grounds of that part of the river still accessible to the running stock. A survey of the river was made by BERG. The gross area of nursery grounds is of the order of 7 sq. km (comprising also a certain amount of less productive areas). This would mean an average smolt production of at least 0.3 per 10 sq. m in this comparatively infertile stream. Now, Canadian investigations indicate smolt production figures of 0.3 to 0.7 smolts per 10 sq. m, varying with fertility and predation (ELSON 1957; cf. MEISTER 1962), and unpublished Swedish experiments in a productive small river in the south of Sweden give figures for the autumn population of large parr of about 0.3 per 10 sq. m on average (Salmon Research Institute). On hand these comparison there seems to be reason to regard the smolt estimate for Indalsälven as fairly good or probably too high if expressed as wild smolts.

b. Total smolt recruitment to the Baltic has been estimated by KÄNDLER (1958) from the percentage return of tagged (hatchery) salmon in the German catches to be of the order of 5 million annually in the years 1955 and 1956 expressed, consequently, in terms of hatchery fish. It is thought that the Swedish rivers contribute something between two thirds and three quarters to the Baltic stock (cf. ALM 1954) and the river Indalsälven roughly 7—8 % of this Swedish share. This would imply a smolt contribution from Indalsälven of 230,000—300,000, a highly conjectural figure, it must be admitted, but in surprisingly good agreement with the results of the internal tagging experiments.

c. The salmon conservation programme for the Indalsälven provides for an annual planting of 320,000 smolt, intended not only to maintain the stock of recent years but to take care also of that part of the original stock subject to damage by earlier power developments in the upper reaches of the salmon section of the river.

The programme has been put into operation gradually, as is evident from the diagram, Fig. 1, which demonstrates also the catch development in some Swedish rivers on hand the official statistical records. A direct comparison is greatly complicated by, *inter alia,* the facts (1) that the catch statistics are very dubious and are not uniform for the few undamaged rivers still available as standards and (2) that the exploitation in the Indalsälven may have changed from the original rate [1] with much gear commercially operated to the present situation where only a few of these are left in the lowest 10 km but they are operating on a concentration of fish. At any rate, there has been an improvement for the Indalsälven catch weight in recent years as the apparent result of the shift from natural recruitment of wild smolts to the systematic planting of hatchery fish. This indicates that the smolt estimate is on the conservative side and is liable to reconsideration in the near future.

The final evaluation of the recruitment capacity of our rivers to be maintained artificially is, however, greatly complicated by several facts that cannot be discussed in detail in the present connection: the nature of the long-term fluctuations in the Baltic salmon stock is not understood and it is not even possible to decide with certainty whether they are to be connected with the stage before or the stage after the smolt part of the life-cycle; if the stock fluctuations reflect fluctuating smolt recruitment to the sea — in any case not likely — the position of our standard year 1953 is of importance in

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[1] About 60 % of the running fish, see CARLIN 1949, LINDROTH 1951.

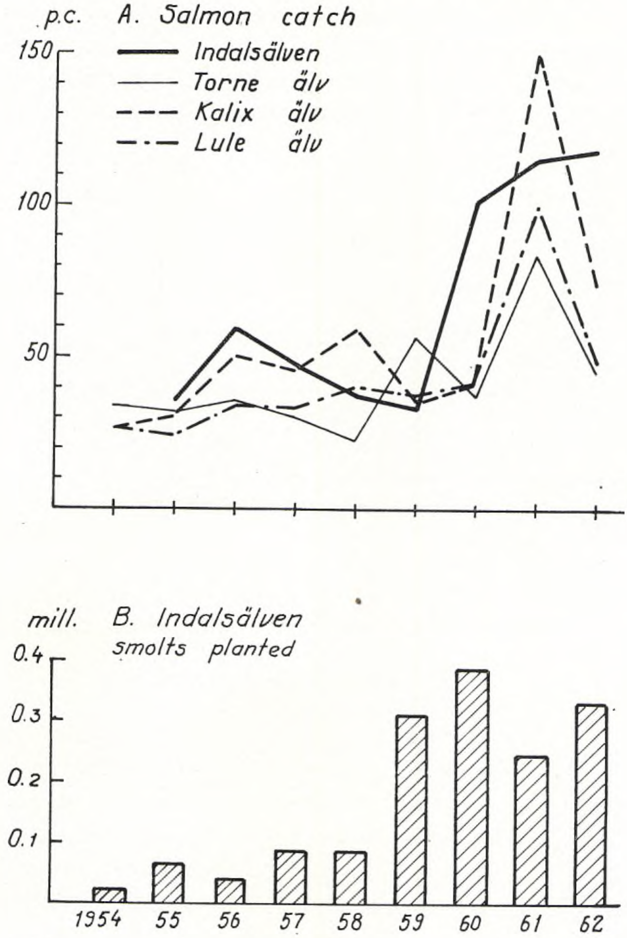

Fig. 1. A. Salmon river catch 1954—62 in Indalsälven and three other rivers expressed as percentage of the mean catch 1916—24, 1932—53 (tons). B. Planting of hatchery smolt-sized parr in Indalsälven in spring 1954—62 (millions).

estimating average conditions; the value of the hatchery fish as compared with the wild smolts from undamaged rivers remains to be studied,[2] and so on. In the prevailing situation it would be premature to enter into a concluding discussion.

Summary

1. The final results of the internal tagging experiments of 1952—55 are reported. They indicate a natural smolt recruitment to the Baltic from the Indalsälven river in the year 1953 of about 230,000 in terms of hatchery smolt-sized parr.

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[2] Such studies have been in progress since 1960.

2. The result is tested against (a) known figures of smolt production per unit area, (b) estimated total Baltic smolt production, and (c) the effect on the Indalsälven salmon catch now artificially maintained on the basis of the smolt figure arrived at. The agreement is in all cases reasonable.

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Addendum.

According to H. PETERSON (personal communication), studying tagging returns and scales in grilse-sized fish at Bergeforsen, true grilse, when surviving, may return to the river after one year and still at grilse size. This could have given a somewhat to high figure for grilse examined 1954 of the smolt year-class 1953 (see table p. 109) in which case the smolt figure would be correspondingly to high.

Studies on planktonic crustacea in thirteen lakes in northern Sweden

By Tom Lötmarker

Contents

Introduction

The effects of regulations[1] on the biological conditions of Scandinavian lakes have been the object of many investigations. Most often it is the changes in the fish populations and the bottom fauna that have been studied. Attention has seldom been paid, however, to the problems of the plankton fauna. The present study is intended to fill this gap and to give an idea of the effects that a regulation may have on the zooplankton.

During the summer of 1957 plankton samples were collected in six regulated and seven unregulated lakes in northern Sweden. The sampling took place once a month during the period June—September. In some of the lakes, however, samples were taken only three times.

Only the plankton organisms of great importance as fish food, the crustaceans, have been subjected to analysis.

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[1] The term "regulation" in this paper, as in other Scandinavian literature, is used in the meaning of "artificial control of the water-level".

As comparatively little is known about the plankton fauna of North-Swedish lakes, the structure of the plankton community has been studied, as well as the vertical distribution and the diurnal migration of some crustacean species. In order to understand possible differences between the lakes, the annual cycle of the different species of plankton must be known. In spite of the absence of winter samples, attempts have been made at establishing the annual cycle of some of the most abundant copepods and cladocerans.

There are, however, many problems connected with the biology and ecology of the crustaceans in question, problems which cannot be solved through field observations alone. Future laboratory experiments might provide complementary information of great interest.

I. Data about the lakes

The geographical situation of the thirteen lakes examined is seen in fig. 1. The lakes Ottsjön, Torrön, Stora Mjölkvattnet, Rengen, Kvarnbergsvattnet, Storsjouten and Borgasjön are situated in the county of Jämtland, whereas the lakes Vojmsjön, Storuman, Storjuktan, Fjosokken, Övre Björkvattnet and Överuman lie in the county of Västerbotten. The depths of the lakes are illustrated by figures and the sampling stations, marked with an arrow, can also be seen (Fig. 2—5).

In table 1, details about the lakes are given regarding altitude, area, maximal depth, mean depth, volume, as well as data of the six regulated lakes. Water level and discharge of the regulated lakes during the period May—October are seen in figure 16.

All the lakes may be classified as oligotrophic.

The temperature, measured on each sampling occasion, has been stated in the diagrams of the vertical distribution of the planktons (Fig. 32—44).

In mid summer, most of the lakes are thermally stratified. Data regarding ice-formation and the break-up of the ice are given in table 2, where it can be seen that in 1957 the break-up of the ice was late.

The air temperature in June was somewhat below the normal. At Östersund the mean temperature was +9.0°C (+11.3) and at Tärnaby +6.5°C (+8.7). The corresponding values for July were +14.5°C (+14.2) and +13.9°C (+12.4) respectively. With the exception of August the summer was rainier than usual.

It should be pointed out that the lakes concerned are situated so far north that the sun does not set until 10 p.m. on June 24th, at about 8.50 p.m. at the beginning of August and at about 7 p.m. at the end of August.

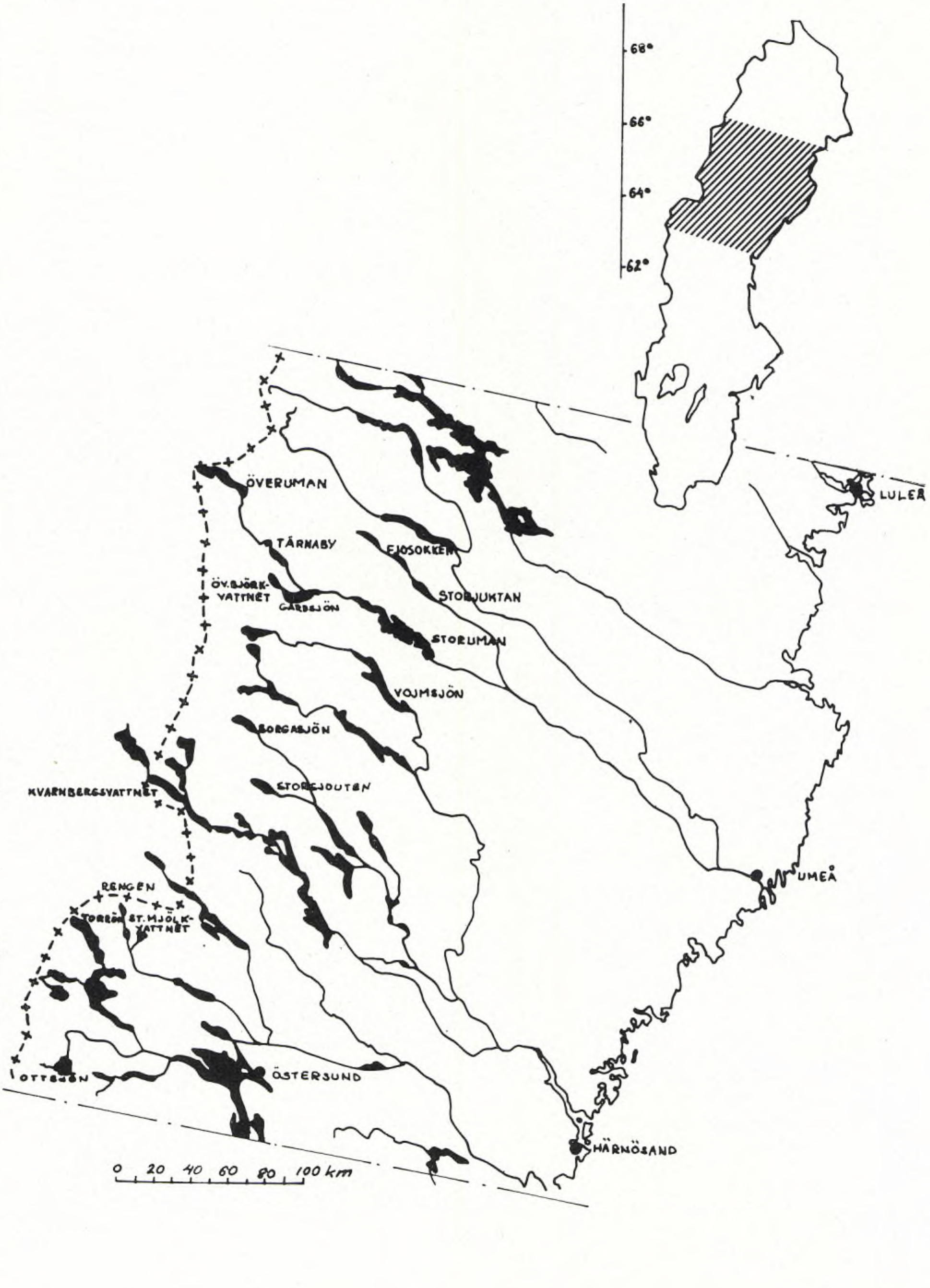

Fig. 1. The geographical situation of the thirteen lakes.

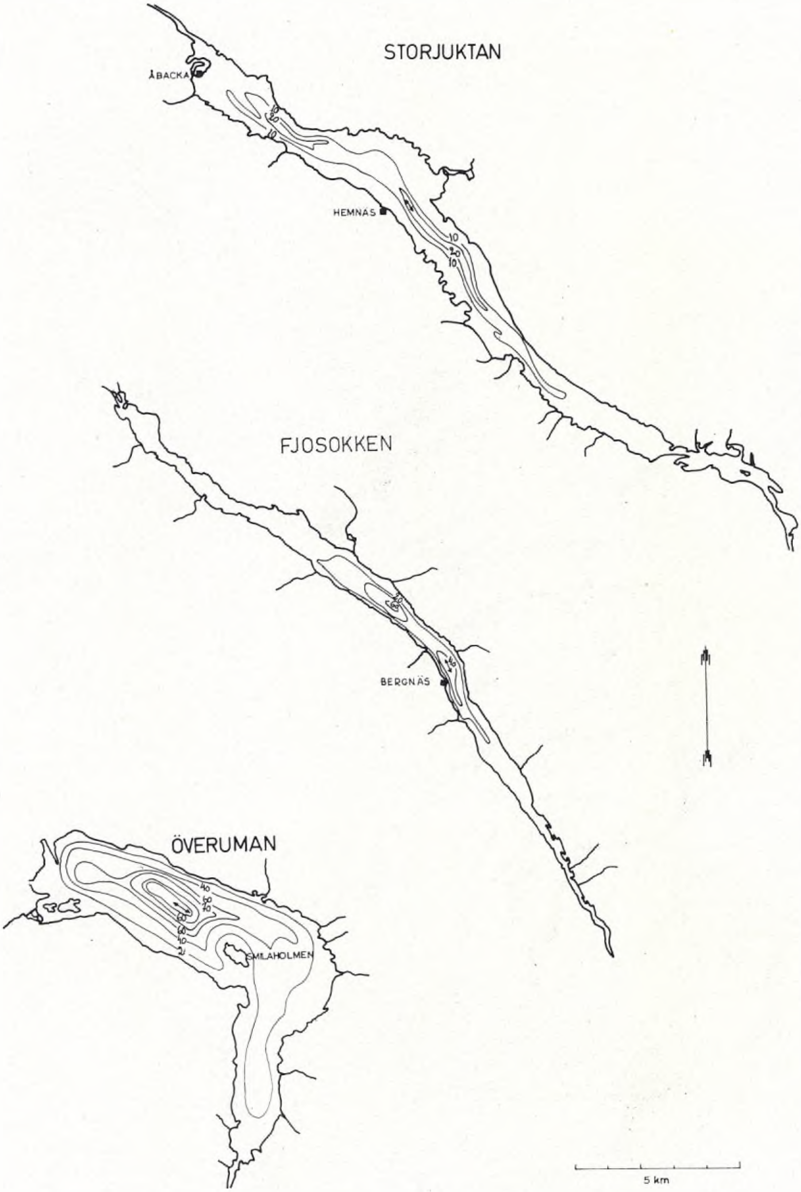

Fig. 2.

Fig. 2—5. Hydrographic maps of the lakes examined. Depths are indicated in metres and the sampling station is indicated by the sign ⟷.

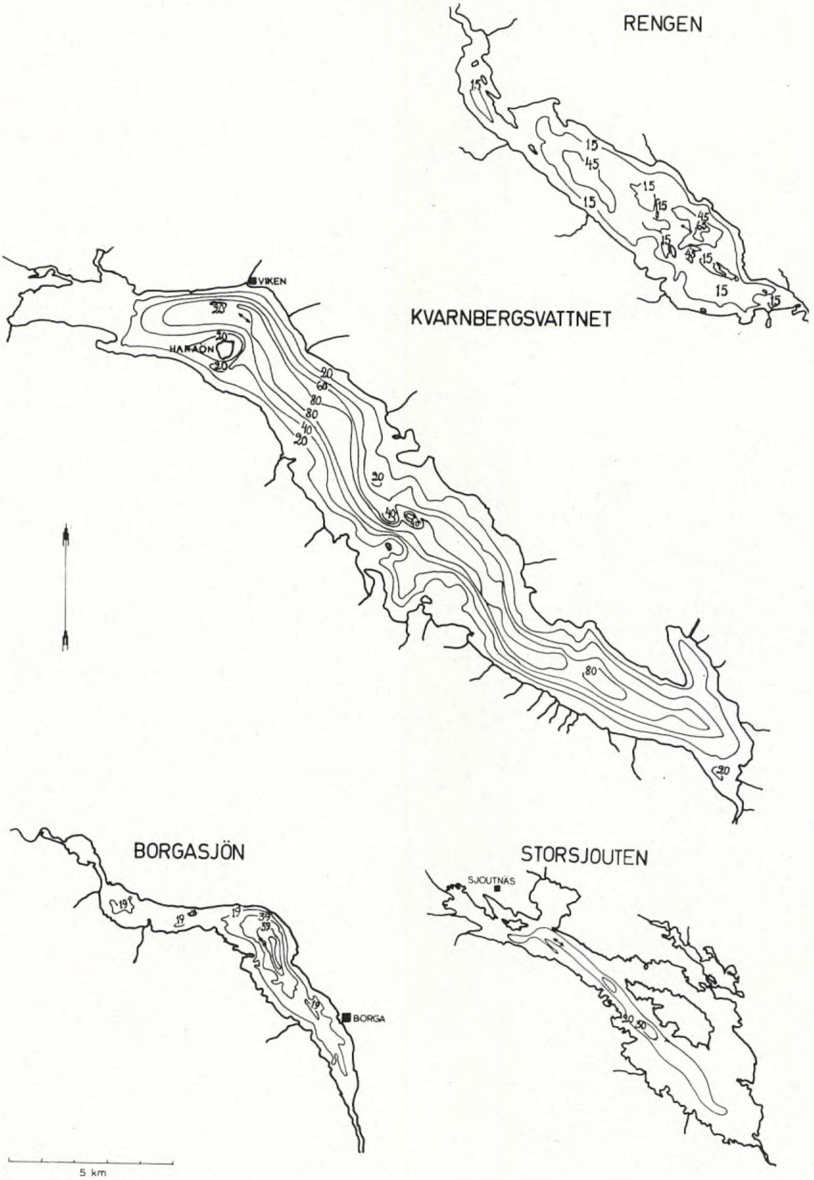
RENGEN
15
45
65
KVARNBERGSVATTNET
VIKEN
HARAÖN
20
40
60
80
BORGASJÖN
19
39
59
BORGA
STORSJOUTEN
SJOUTNÄS
20
50
5 km

Fig. 3.

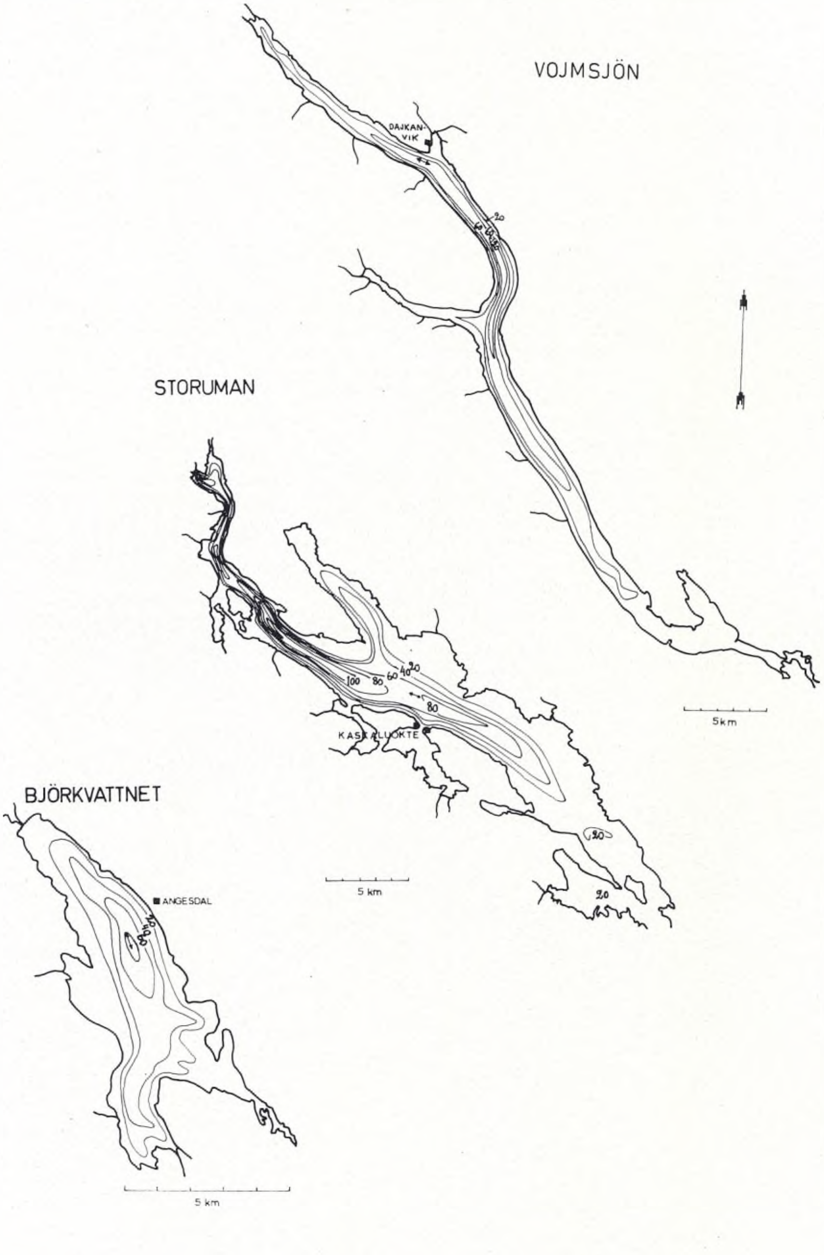
VOJMSJÖN
DAJKAN-VIK
20
40
5km
STORUMAN
100
80
60
40
20
80
KASKALUOKTE
20
20
5 km
BJÖRKVATTNET
ANGESDAL
5 km

Fig. 4.


OTTSJÖN
17
29
19
TORRÖN
111
71
31
31
31
31
51
91
71
51
71
31
ST. MJÖLKVATTNET
HIMMELSRAFTEN
5 km

Fig. 5.

Table 1. Physical data of the thirteen North-Swedish lakes according to SMHI (The Swedish Meteorological and Hydrological Institute) and limits of regulation for the six regulated lakes according to Indalsälvens vattenregleringsföretag and K. Vattenfallsstyrelsen.

Name of lake	Altitude, metres	Area km²	Approx. max. depth, metres	Mean depth, metres	Volume, million m³	First year of regulation	Limits of regulation 1957	
							Number of metres above (+) and below (—) mean water level	
Övre Björkvattnet	393	29.13	65.5	30.1	878.0	—	—	—
Borgasjön	451	10.91	70	20.2	220.0	1952	+16	— 1
Fjosokken	410	13.45	62.2	15.7	210.5	—	—	—
Kvarnbergsvattnet	312	66.344	98	41.0	2720.0	1940	+ 0	— 8.5
Stora Mjölkvattnet	544		No information	available		1944	+10	— 0
Ottsjön	494	15.59	30	10.3	161.3	—	—	—
Rengen	345	19.705	65	21.0	414.0	—	—	—
Storjuktan	399	26.65	32.3	8.1	216.4	—	—	—
Storsjouten	443	21.98	32.6	9.2	202.2	1947	+ 7	— 3
Storuman	349	163.0	123.5	25.7	4185.0	—	—	—
Torrön	411	95.2	115	35.5	3380.0	1935	+ 6	— 5
Vojmsjön	413	79.25	130	39.3	3114.0	1949	+ 2	— 3
Överuman	520	75.0	78.8	20.6	1544.0	—	—	—

Table 2. Dates for the breaking up of the ice and the formation of a new ice-cover according to SMHI and a list of the exploited fish populations common in the lakes examined according to The Institute of Freshwater Research, Drottningholm (The names of the most common species are printed in italics).

	Dates for the breaking up of ice and the formation of a new ice-cover			Dates for the breaking up of the ice 1957	Fish fauna
	Period	Breaking up of ice	Formation of ice-cover		
Övre Björkvattnet	1909/10—1950/51	30/5	5/12	3/6	*Char,* Trout
Borgasjön	1913/14—1959/60	28/5	25/11	31/5	*Char,* Trout, Burbot
Fjosokken	1950/51—1957/58	1/6	14/11	30/5	*Whitefish,* Grayling, Trout, Perch, Pike, Burbot
Kvarnbergsvattnet ...	24 winters until 1938/39	26/5	—	27/5	*Char,* Trout
	9 „ „ 1939/40—47/48	27/5	—	—	
	10 „ „ 1948/49—57/58	23/5	—	—	
	26 „ „ 1938/39	—	29/12	—	
	8 „ „ 1939/40—47/48	—	4/1	—	
	10 „ „ 1948/49—57/58	—	1/1	—	
Stora Mjölkvattnet ...	No information available				*Char,* Trout, Burbot
Ottsjön	1955—1961 (6 years)	26/5	—	27/5	*Char,* Trout, Grayling, Burbot
	1954—1960 (7 „)	—	24/11	—	
Rengen	1922/23—1957/58	21/5	7/12	25/5	*Trout,* Char, Burbot
Storjuktan	1908/09—1950/51	25/5	27/10	29/5	*Whitefish,* Grayling, Trout, Char, Pike, Perch, Burbot, Cyprinids
Storsjouten	1944/45—1959/60	24/5	21/11	—	*Char,* Trout
Storuman	1867/68—1950/51	29/5	5/12 [1]	28/5	*Whitefish,* Grayling, Char, Trout, Perch, Pike, Burbot
Torrön	1936—1957	24/5	22/12	29/5	*Char,* Trout, Grayling, Burbot
	1936—1957	26/5	31/12	—	
Vojmsjön	1870/71—1958/59	28/5	22/12	28/5	*Whitefish,* Grayling, Trout, Char, Perch, Pike, Burbot
Överuman	1916/17—1947/48	12/6	4/12	13/6	*Char,* Trout

[1] No information available for the period 1921/22—1946/47.

II. Methods

It is a well-known fact that most plankton crustaceans make diurnal migrations, which may be more or less marked and which manifest themselves in an uneven vertical distribution of the animals. For a long time it was supposed that the horizontal distribution was uniform. In recent years, however, several authors (RAGOTZKIE-BRYZON 1953, TONOLLI 1956, COLEBROOK 1960) have been of opinion that the zooplankters may occur in patches, a fact which has been ascribed to different factors. These circumstances must be taken into account when collecting plankton samples.

The samples from the thirteen lakes have all been taken at night by horizontal hauls at one station in each lake.

The plankton was taken by means of the Clarke-Bumpus closing-type plankton sampler (CLARKE-BUMPUS 1940, WELCH 1948). Before the fieldwork was begun, the instrument with its propeller-counter mechanism was calibrated in terms of the number of litres of water filtered per propeller revolution. The result was 5.35 l/revolution. The meshes of the plankton net were of the size 0.158 mm. With finer meshes there is a risk of the net clogging and preventing the sampler from functioning satisfactorily. The mesh size given will, however, let a number of rotifers pass through the filter. For this reason the rotifers have not been taken into consideration.

In each lake the sampling took place at one and the same station, generally at the middle of the lake and in a depth basin showing a fairly constant depth for some 400 metres, thus enabling horizontal hauls.

The sampling was carried out from a rowing boat provided with a small outboard motor. The work was begun at 10 p.m. and terminated by 1 a.m. at the latest. Horizontal hauls were made at the following levels: 2, 5, 10, 15, 20, 30, 40 metres and so on. In order to avoid damaging the sampler against objects at the bottom of the lakes, the vertical series were all interrupted at a height of about 10 metres from the bottom. This means that the plankters occupying the layers close to the bottom have been omitted. Owing to the diurnal migration of the crustaceans, this layer will, however, contain few individuals during the night the source of error will be less significant when the samples are taken at night than would be the case if they were taken by day. Night samples are preferable for yet another reason. Results show that larger plankton forms, which can see the sampler in daylight, are less numerous in samples taken by day than in samples taken in the same profile at night (SOUTHERN and GARDINER 1926, RICKER 1937).

To have the sampler operating at the depth required, a table had been drawn up in advance, indicating the necessary length of wire for each level, calculated at a fixed angle between the wire and the vertical plane. This angle was permanently checked during the towing period. Even if the sampler were not moving exactly at the intended level, the results from the different depths and the different lakes would still be comparable, as for each level the length of wire was the same in all the lakes.

With a few variations the average water volume represented by a sample is about 2 m^3. The animals have been preserved in 4 % formaldehyde. In connection with the sampling the temperature was taken at each station by a Ruttner water sampler with built-in thermometer.

It will be evident from what has been said that each sample would contain such a great number of animals that it would hardly be possible to count them all. The samples were therefore fractioned by a whirling apparatus — of the type described by KOTT (1953) — which on repeated testing occasions has proved to work satisfactorily. $^1/_{10}$ of each sample has been counted.

The material comprises about 450 samples distributed over 48 vertical series.

Counting and identification were done in a small plastic chamber using a dissecting microscope. It was considered that a simple division into species would be insufficient for the adequate treatment of the material, and a subdivision into different stages of development has therefore been made in order to show the seasonal cycle of the various species during the summer months. The nauplii have been divided into *Centropagidae* and *Cyclopidae*. There has been no division into nauplii and metanauplii. The subdivisions of the copepodids are young (stage I—III) and old (stage IV—V) individuals and those of the adult copepods are males, females and egg-carrying females (*Cyclops, Diaptomus*). As regards *Daphnia* a division has been made into egg-carrying and not egg-carrying females, males and juveniles. As concerns *Bosmina* only egg-carrying and not egg-carrying females and males have been taken into consideration, owing to the difficulty of distinguishing juveniles and adults. *Holopedium* has only been divided into egg-carrying and not egg-carrying individuals. The remaining cladocerans have only been identified as to species.

The results are shown in tables and diagrams. The diagrams that show the vertical distribution (Fig. 32—44, individuals/m^3) have been drawn up in the way usual in works on plankton, that is by reproducing the distribution by means of the third root of values. There have been some difficulties in expressing the density of the standing crop of zooplankton as it has not been possible to take samples at every metre between the surface and the bottom of the lake. The number of individuals that there are under a certain unity of the surface has been calculated by interpolating between the levels at which samples have been taken. This method is a little uncertain but represents the only way to work. The diagrams show the number of individuals/dm^2 (Fig. 8—15, 17—18). The composition of the zooplankton community has been illustrated by circle diagrams where the sizes of the surfaces are in proportion to the percentages of the copepods and the cladocerans (Fig. 19—31).

III. The composition of the crustacean fauna

As mentioned earlier the present study concerns only the crustaceans. There have been found, in all, 11 species of *Copepoda* and 11 species and subspecies of *Cladocera*.[1] Chydorids have not been taken into account and as a rule they have not been identified as to species. They have only been found in very small numbers. The distribution of the different species in the lakes examined is shown in table 3.

Copepoda

Of cyclopoids four species have been found. *Cyclops scutifer* SARS is very numerous in many of the lakes investigated. A few specimens of *Mesocyclops obsoletus* KOCH and *M. oithonoides* SARS have been found in Storjuktan and Storuman. *Pachycyclops annulicornis* KOCH has occurred in samples from four lakes.

The genus Diaptomus is represented by *Diaptomus denticornis* WIERZEISKI, *D. graciloides* LILLJEBORG, *D. laciniatus* LILLJEBORG and *D. laticeps* SARS. From table 4 it is seen that *D. graciloides* and *D. laticeps* act as vicarious species. These species are totally absent only in the samples from Borgasjön where, instead, *D. denticornis* and *D. laciniatus* are found in small numbers. In his papers on Kultsjön and Ransaren AXELSON (1957, 1961 a) has pointed out that two lakes which are close to each other in the same water system present two different species of *Diaptomus* (*D. graciloides* and *D. laticeps*). This is the case with some lakes in the water system of the river Ume älv. Only *D. laticeps* has been found in Överuman, where it is, however, abundant. In Övre Björkvattnet, which lies below Överuman in the same water system, there are both *D. graciloides* and *D. laticeps,* the latter, however, in small numbers. Some samples from Gardsjön, which lies still further down, have shown that while *D. graciloides* is the dominating species *D. laticeps* is also found. In Storuman, however, the genus seems to be represented only by *D. graciloides*.

According to EKMAN (1904) *D. graciloides* is an immigrant from the south which has followed the ice as it receded after the last ice-age. *D. laticeps,* on the other hand, is considered to have come from the east (RYLOV 1935, THIENEMANN 1950). One might then expect *D. graciloides,* which was probably the first of the two species to invade the area in question, to have spread as far as to Överuman and *D. laticeps* to be more common further down in the water system. The results, however, show a completely contrary distribu-

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[1] In order to avoid confusion and as no modern revision of the taxonomy of the genus Daphnia has been undertaken as regards European Daphnia, the nomenclature according to RYLOV (1935) has been used. Several of the subspecies mentioned by RYLOV are in fact species and are treated as such in this paper.

Table 3. Planktonic crustaceans observed in the thirteen lakes.
(××× = common, ×× = less common, × = rare)

	Övre Björk-vattnet	Borgasjön	Fjosokken	Kvarnbergs-vattnet	Stora Mjölk-vattnet	Ottsjön	Rengen	Storjuktan	Storsjouten	Storuman	Torrön	Vojmsjön	Överuman
Copepoda:													
Cyclops scutifer SARS	×××	×××	××	×××	×××	×××	×××	××	×××	×××	×××	×××	×××
Mesocyclops absoletus KOCH	—	—	—	—	—	—	—	×	—	—	—	—	—
Mesocyclops oithonoides SARS	—	—	—	—	—	—	—	—	—	×	—	—	—
Pachycyclops annulicornis KOCH	—	—	—	—	—	×	×	×	—	—	×	—	—
Diaptomus denticornis WIERZEJSKI	—	×	—	×	—	—	—	—	×	—	××	—	—
Diaptomus graciloides LILLJEBORG	×××	—	×××	—	—	—	×××	×××	—	×××	—	×××	—
Diaptomus laciniatus LILLJEBORG	—	×	—	×	××	—	—	—	—	—	—	—	—
Diaptomus laticeps SARS	×	—	—	×××	××	×××	×	—	××	—	××	—	×××
Heterocope appendiculata SARS	—	—	××	—	—	—	—	××	—	××	—	××	—
Heterocope borealis FISCHER	—	—	—	—	—	—	—	—	—	—	—	—	×
Heterocope saliens LILLJEBORG	×	××	—	××	—	×	×	—	××	—	×	—	—
Cladocera:													
Daphnia cristata cristata SARS	—	—	×××	—	—	—	—	×××	—	××	×	×××	—
Daphnia cristata longiremis SARS	—	×	—	—	—	—	×	—	×	—	×	—	—
Daphnia longispina hyalina LEYDIG	×××	×××	—	××	—	×××	××	—	×××	—	××	—	××
Daphnia longispina longispina O. F. MÜLLER	—	—	—	—	—	—	××	—	—	—	××	—	—
Ceriodaphnia quadrangula O. F. MÜLLER	—	—	—	—	—	—	—	×	—	—	—	—	—
Sida crystallina O. F. MÜLLER	×	—	—	—	—	—	—	—	×	×	—	—	×
Bosmina coregoni BAIRD	×××	×××	×××	×××	×××	×××	×××	×××	×××	×××	×××	×××	×××
Holopedium gibberum ZADD	××	×××	×××	×××	×××	×××	×××	×××	×××	×××	×××	×××	×××
Polyphemus pediculus LINNÉ	×	—	×	—	—	×	×	×	×	×	×	×	—
Bythotrephes longimanus LEYDIG	×	×	—	×	×	×	×	—	×	—	×	—	—
Leptodora kindtii FOCKE	—	—	×	—	—	×	×	×	×	×	—	×	—

Table 4. Grouping together, to the left, lakes with a cold stenothermal fauna and, to the right, lakes with an eurythermal fauna.

	Överuman	Ottsjön	Stora Mjölk-vattnet	Torrön	Storsjouten	Kvarnbergs-vattnet	Borgasjön	Övre Björk-vattnet	Rengen	Storuman	Vojmsjön	Storjuktan	Fjosokken
Diaptomus denticornis	—	—	—	××	×	×	×	—	—	—	—	—	—
Diaptomus graciloides	—	—	—	—	—	—	—	×××	×××	×××	×××	×××	×××
Diaptomus laciniatus	—	—	××	—	—	×	×	—	—	—	—	—	—
Diaptomus laticeps	×××	×××	××	××	××	××	—	×	×	—	—	—	—
Heterocope appendiculata	—	—	—	—	—	—	—	—	—	××	××	××	××
Heterocope borealis	×	—	—	—	—	—	—	—	—	—	—	—	—
Heterocope saliens	—	×	—	×	××	××	××	×	×	—	—	—	—
Daphnia cristata cristata	—	—	—	×	—	—	—	—	—	××	×××	×××	×××
Daphnia cristata longiremis	—	—	—	×	×	—	×	—	×	—	—	—	—
Daphnia longispina hyalina	××	×××	—	××	×××	××	×××	×××	××	—	—	—	—
Daphnia longispina longispina	—	—	—	××	—	—	—	—	××	—	—	—	—

tion. It is possible that *D. graciloides* has existed in Överuman after the ice-age, in which case *D. laticeps* has proved to be the stronger species of the two.

Ekman (1922) has drawn up a table showing the sensitivity to temperature of some pelagic copepods and cladocerans. It indicates that *D. laticeps* is bound to lakes with cold water, whereas *D. graciloides* appears also in lakes with warm water. One might then think that *D. graciloides* could not compete with *D. laticeps* in lakes with low water temperatures. This assumption is to some extent supported by the results achieved. No specimens of *D. graciloides* have occurred in the lakes where *D. laticeps* is abundant, while *D. laticeps* is found in small numbers in lakes where *D. graciloides* dominates. This presence is probably accounted for by *D. laticeps* being brought to the lakes by the inflow from a neighbouring lake where the species is found in great abundance.

The distribution of the three species of the genus *Heterocope* is similar. *Heterocope appendiculata* Sars has not occurred in any of the mountain lakes and according to Ekman it is an eurythermal species, while the two others *H. borealis* Fischer and *H. saliens* Lilljeborg are typical cold stenothermal species. *H. saliens* has been found in all the mountain lakes except Överuman, where *H. borealis* takes its place. Comparisons show that the three lakes Överuman — Övre Björkvattnet — Storuman which, as mentioned, are in the same water system contain respectively *H. borealis* — *H. saliens* — *H. appendiculata*.

The cold stenothermal species *D. laticeps* and *H. saliens* (or *H. borealis*) always occur together in the plankton community. Övre Björkvattnet and Rengen containing *D. graciloides, D. laticeps* and *H. saliens* form a transition to the lakes containing *D. graciloides* and *H. appendiculata*. Ekman (1904, 1922) includes also *D. denticornis* and *D. laciniatus* in the category of cold stenothermal animals and the results achieved show, in fact, that these species only occur in lakes with other cold stenothermal species (Table 4).

Cladocera

The *Daphnia* genus is represented by *Daphnia cristata* subsp. *cristata* Sars, *D. cristata* subsp. *longiremis* Sars, *D. longispina* subsp. *hyalina* Leydig and *D. longispina* subsp. *longispina* O. F. Müller.

According to Rylov (1935) *D. cristata cristata* is an eurythermal form found in Northern and Central Europe. It has been found in great numbers in four lakes and sporadically in one lake. *D. cristata longiremis* has occurred in very small numbers in four lakes. It is generally described as being a pronouncedly cold stenothermal animal. *D. longispina hyalina* is found in most lakes (eight) and most often farily abundantly. It is not so stenothermal as *D. cristata longiremis* (Ekman 1922). In the lake where it has been found, *D. longispina longispina* has been represented by *var. cavifrons* SARS.

Bosmina coregoni BAIRD (according to the classification of *Bosmina* by BURCKHARD, 1941) is very common in all the lakes. It occurs together with *Holopedium gibberum* ZADD. These two species together with *Daphnia* generally form the main part of the cladocerans of the plankton community.

The remaining cladocerans, *Sida crystallina* O. F. MÜLLER, *Polyphemus pediculus* LINNÉ, *Bythotrephes longimanus* LEYDIG and *Leptodora Kindtii* FOCKE only occur in small numbers.

The cladocerans show a distribution that is in many respects similar to that of the copepods. *Daphnia longispina hyalina* is common in all the mountain lakes except Stora Mjölkvattnet where *Daphnia* is quite missing, while *D. cristata cristata* has only been found in the lakes situated further down in the water systems. In most of the lakes there were small quantities of *Polyphemus pediculus* and *Leptodora Kindtii*. The distribution of the cladocerans is illustrated in table 4.

It can thus be established that the lakes investigated can be divided into two groups as far as the composition of the crustaceans is concerned. One group comprises lakes containing the cold stenothermal species *Diaptomus laticeps, Heterocope saliens* (or *H. borealis*), *Daphnia longispina hyalina,* while the other group has an eurythermal plankton fauna with *Diaptomus graciloides, Heterocope appendiculata, Daphnia cristata cristata.* Common to the two groups are *Cyclops scutifer, Bosmina coregoni* and *Holopedium gibberum.*

LÖFFLER (1953) has found that in the upper part of the water system of the river Faxälven there are cold stenothermal animals, while further down there are eurythermal species. It might then be concluded that the present distribution is due only to the temperature tolerance of the species. In his account of the species composition prevailing in some water systems in the north of Sweden, EKMAN (1922) has stated that this is not the case. The temperature factor must not be disregarded but the geographical distribution of the species is undoubtedly regulated by a number of factors. A more thorough knowledge of the biology of every species and of the composition of the plankton fauna in different North-Swedish lakes is required before the causes of the somewhat irregular distribution displayed by many plankton crustaceans can be satisfactorily explained.

IV. The structure of the plankton community

In a previous chapter an account was given of the different species found in the lakes. In this chapter two questions will be treated, both of which concern the composition of the plankton community; namely, the number of species occurring together in a plankton community and the relations of dominance between the species. Very little attention has been given to these problems. PENNAK (1957) has discussed them in a paper where he compares his results from 27 lakes in Colorado with data from 42 other lakes, most of which are situated outside the United States. Since PENNAK has stated that there are certain differences between the two groups of lakes regarding the composition of the plankton community, it might be of interest to compare the results from the thirteen lakes in northern Sweden.

What in this case gives perhaps special interest to a close examination of the composition of species is the question of the influence of the regulation on zooplankton. It is well known that a change in environment is reflected by the composition of a plant or animal community. To find out what species are affected by the regulation of a lake, it would be of importance not only to calculate the number of individuals but also to compare the plankton communities of the lakes.

The number of crustacean species making up the plankton community

It must be borne in mind that the following is an account of the momentary composition of the plankton community, such as it appears in one vertical series of samples at any one time.

As seen in table 5 three species of *Copepoda* have been found in most of the vertical series. They were *Cyclops scutifer,* one *Diaptomus* and one *Heterocope* species. In the series containing two copepods, *Cyclops scutifer* was always present together with one diaptomid; there were never two diaptomids. When there were four or five species of *Copepoda,* one or two cyclopoids were together with two diaptomids and one species of *Heterocope.* Two species of *Heterocope* were never present in the same lake.

As regards *Cladocera* the number of species present at any one time was four or five. In most cases one or two species of *Daphnia* occurred together with *Bosmina coregoni* and *Holopedium gibberum,* often associated also with one or more of the following cladocerans: *Polyphemus pediculus, Bytho-*

Table 5. Number of species present at any one of the 48 samplings during June—September.

	Number of species present at any one time									Total number of species
	1	2	3	4	5	6	7	8	M	
Copepoda	—	9	22	16	1	—	—	—	3.2	11
Cladocera	—	1	4	16	15	7	3	2	4.8	11

Table 6. Mean number of species making up the zooplankton community momentarily present in the lakes. Comparison with PENNAK (1957).

	Copepoda	Cladocera
27 lakes in Colorado	1.3	1.6
42 lakes mostly located outside U.S.A.	2.7	2.8
13 lakes in northern Sweden	3.2	4.8

trephes longimanus, Leptodora Kindtii. Sida crystallina and *Ceriodaphnia quadrangula* also occurred but only in a few samples. The series containing two species, *Bosmina coregoni* and *Holopedium gibberum,* is from Stora Mjölkvattnet, where *Daphnia* is absent.

The zooplankton community is thus made up of a small number of crustacean species. During June—September the mean number for *Copepoda* is 3.2 species and for *Cladocera* 4.8 species. According to PENNAK the mean numbers do not vary markedly during the course of the year. It would thus be possible to compare the results from the lakes in northern Sweden with the results arrived at by PENNAK (1957).

The series of samples taken from the lakes of northern Sweden contain more species of *Copepoda* as well as of *Cladocera* than the lakes described by PENNAK (Table 6). The Colorado lakes show the lowest mean numbers and, according to PENNAK, this is owing to the small size of the lakes. Large and deep lakes contained more copepod species while there was no significant difference in number of species between oligotrophic and eutrophic lakes. Nor could PENNAK find that differences in latitude or altitude were of any importance. Tropical, temperate and subarctic lakes were all strikingly similar.

Most of the lakes in northern Sweden are large as well as deep, which may to some extent explain the higher mean number of species in these lakes, especially as regards the copepods. To some extent the differences also reflect the methods of sampling. Numerically the plankton community is, as a rule, dominated by two species (see below), a copepod and a cladoceran. There is reason to believe that other species, which are not so common, are missing in samples taken by an instrument that filtrates only a small quantity of water. The short summers of northern Sweden must also be taken into account as they bring about a concentration of the development of the different species within a considerably shorter period than what is normal further south. There is thus greater possibility, in these lakes, of finding several copepod species at one time. As most species develop resting eggs during the autumn and winter, the possibilities of spreading are also greater in northern areas.

In this connection the occurrence of two diaptomids in the same lake should be mentioned. It has often been stated that the occurrence of two species so closely related is rare, as there would be competition between them for food. Out of the thirteen lakes examined, six have been found to have two *Diaptomus* species and one lake three species. *D. graciloides* and *D. laticeps* are the species that have most often been found together and the former species has always been numerically dominating. As *D. laticeps* is somewhat bigger and more robust than *D. graciloides* there is probably no competition for food between them (HUTCHINSON 1951, FRYER 1954). The two diaptomids existed together only in lakes which are not extreme mountain lakes and in an earlier chapter it was considered that *D. laticeps* was probably brought there by the inflow from lakes situated in the upper part of the water system.

Diaptomus denticornis and *D. laciniatus* have always been found in lakes with *D. laticeps* except in Borgasjön, where neither *D. laticeps* nor *D. graciloides* have been found. Both species are cold stenothermal according to EKMAN (1904). They have never been found in great numbers perhaps because they reach their maximal development only later in the year. The first individuals of both species have appeared in the middle of August, when *Diaptomus laticeps* decreases in number.

Species dominance

When quantitative plankton samples are analyzed, it is generally observed that one species of *Copepoda* and one cladoceran are very abundant and numerically dominant over the other species of *Copepoda* and *Cladocera*. Moreover, throughout the year, there are great variations in the samples in the respective percentage of copepods and cladocerans. The development of the different species is cyclic and the species that is dominant on one occasion is represented a short time before or after by only a few individuals. The samples of one vertical series show that the dominant species seldom accounts for less than 50 % of all the copepods or all the cladocerans.

The composition of the zooplankton community in the lakes during June—September is illustrated by diagrams (Fig. 19—31).

It is not only variations in the course of development of the plankton species that bring about the changes in the zooplankton community. Account must also be taken of the natural changes that take place in a lake during the summer (e.g. temperature and phytoplankton). The probable reason why during a particular period certain species dominate is presumably that they have genetic, morphological, physiological or ecological features which enable them to utilize their habitat more efficiently than other species during the same period (PENNAK 1957).

If the thirteen lakes are compared as to the percentage composition of the plankton community some common features are found in spite of certain differences between the lakes. In June there is a very high percentage of copepods in the samples. The cladocerans are, as a rule, abundant in July and August but even in September they may represent a high percentage in some lakes. In most lakes the copepods dominate on average over the cladocerans during the four summer months. If all the lakes are considered the mean figures are: *Copepoda* 72 % and *Cladocera* 28 %. For the regulated lakes only, the corresponding figures are 78 % and 21 % respectively, the percentage of cladocerans being thus lower. A close examination of the diagrams indicate that only in Stora Mjölkvattnet and Storsjouten is the percentage of cladocerans comparable with the values of many of the unregulated lakes. In the other regulated lakes the contribution to the plankton community of copepods, especially *Cyclops scutifer,* is striking. The effect of the regulations of lakes on the plankton crustaceans will be considered in a following chapter.

A calculation of the relations between the two main groups of *Copepoda* gives the following mean figures valid for all the lakes: *Centropagidae* (*Diaptomus* and *Heterocope*) 39 % and *Cyclopidae* 61 %.

In regard to the composition of the copepod fauna there are certain differences between the lakes owing to differences in the annual cycle of the species (see a following chapter) which give rise to divergencies in the composition of the copepod populations.

From the diagrams, however, it is evident that the copepod fauna is generally dominated by one species, often *Cyclops scutifer.*

Owing to the difficulties in identifying the species of nauplii and copepodids, the copepods have been divided into two groups: *Centropagidae* and *Cyclopidae,* while every species of *Cladocera* has been represented in the diagrams illustrating the percentage composition of the plankton community. As is seen from the diagrams the main portion of *Cladocera* consists in all lakes of *Bosmina coregoni.* Often it entirely dominates the other species, such as *Daphnia c. cristata, Daphnia longispina hyalina* and *Holopedium gibberum.*

In the majority of samples the most abundant species has accounted for more than 50 % of all the cladocerans. The mean figure for all the lakes is 66 %. The second most abundant species accounts for 26 % on an average and for all other species present the mean figure is 8 % (Table 7).

Table 7. Percentage composition of *Cladocera.* Comparison with PENNAK (1957).

	Most abundant species	Second most abundant species	All other species present
27 lakes in Colorado	84.7	12.8	2.5
22 lakes mostly located outside U.S.A.	72.9	21.3	5.8
13 lakes in northern Sweden	66.0 (68.0)	26.0 (26.4)	8.0 (5.6)

The percentage composition of cladocerans in the North-Swedish lakes corresponds fairly well with PENNAK's findings (1957). Two species only account for more than 90 % of all the cladocerans of a vertical series. The data within parentheses referring to the unregulated lakes differ slightly from the mean figures of all the lakes. PENNAK assumes the relations to be 78 % — 17 % — 5 % for a typical lake. The percentage of the dominating species is somewhat lower (66 %) in the thirteen Swedish lakes, while the percentage of the next numerous species is higher (26 %).

It must, however, be borne in mind that the values for the thirteen lakes are based on samples taken during the summer months only when one may expect to find the greatest number of species and when there are likely to be quick changes in the composition of the plankton community. Samplings may therefore have taken place during periods when a dominating species is being replaced by another, both species thus being abundant in the samples.

The results show clearly, however, the relations of dominance prevailing among the species of a cladoceran population. The relations between the most numerous species and the next most numerous vary from lake to lake, but together they account for more than 90 % of all the individuals. As mentioned, the same conditions are true of the copepods.

V. The vertical distribution

The vertical distribution of crustaceans is intimately connected with their diurnal migration. It has long been known that during the night the crustaceans are found mainly close to the surface while in daytime they spread to deeper layers. The migration of different species has been studied by many biologists who have given various explanations of the phenomenon. Surveys of results achieved have been published by CUSHING (1951) and BAINBRIDGE (1961).

Observations on the diurnal migrations of some pelagic crustacean species

As very little is known about the vertical migration of some of the species dealt with in this paper, an investigation has been carried out in Locknesjön, a lake 20 kilometres south of Östersund in the county of Jämtland. The species obtained in quantities large enough to show the vertical distribution at different hours were *Diaptomus graciloides, Daphnia cristata cristata,* and *Bosmina coregoni, Cyclops* only occurred as nauplii, which in all the series were most numerous in the samples taken between 20 and 23 metres deep. Samples were taken on August 30th and 31st, at 11 a.m., 3 p.m., 7 p.m., 11 p.m. and 6 a.m. Sunset was then at about 7 p.m. and sunrise at about 4.30 a.m.

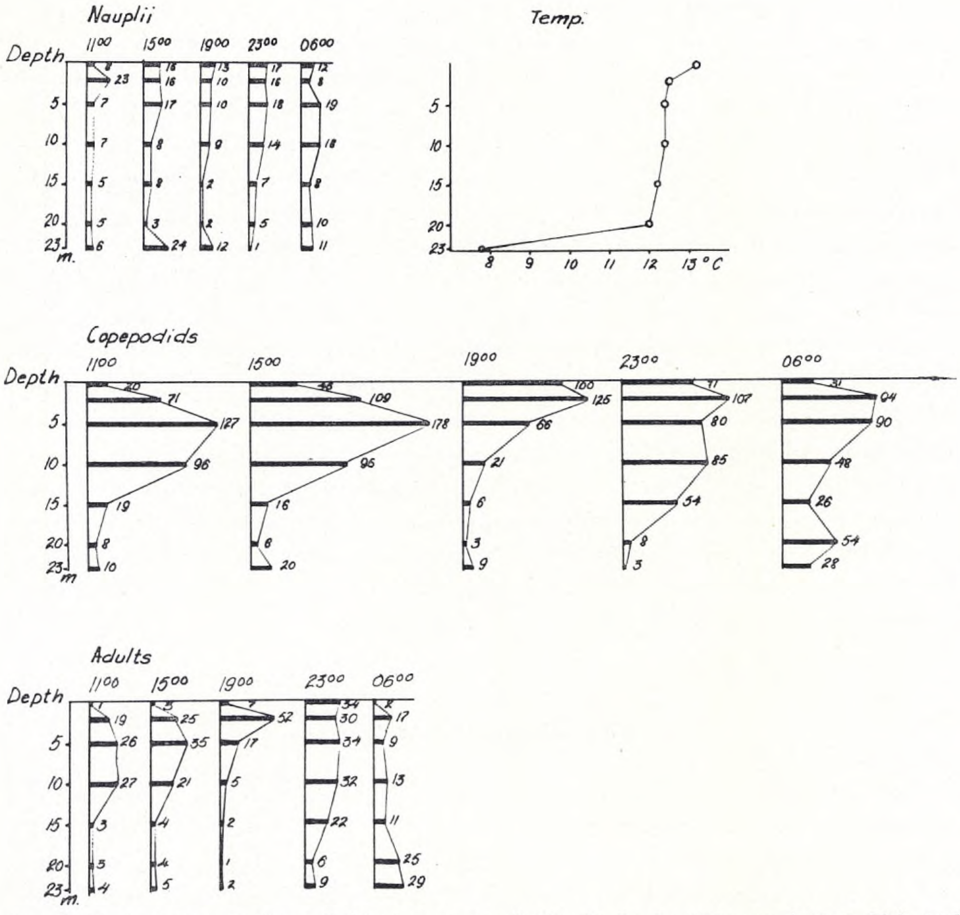


Fig. 6. Vertical distribution of *Diaptomus graciloides* in Locknesjön on August 30th and 31st, 1961. (Individual/5.3 l.)

The weather was calm and there were no clouds. In order to faciliate the counting of all the animals in the samples a sampler with a capacity of 5.3 litres (see LINDSTRÖM, 1952) was used.

During the first series of samples the water temperature was measured. As the temperature curve shows, fig. 6, the water of the lake is mostly homotherm. Only a layer at the bottom has a temperature considerably lower than the rest of the lake. A check made a few days later and at smaller intervals showed that it is a layer only a few decimetres deep at the bottom.

The vertical distribution as it was found at the different hours is shown in fig. 6 and 7.

As seen from the diagrams the vertical distribution of the three species shows almost the same pattern. During the afternoon there is an ascent towards the surface, which results in a great concentration of animals in the

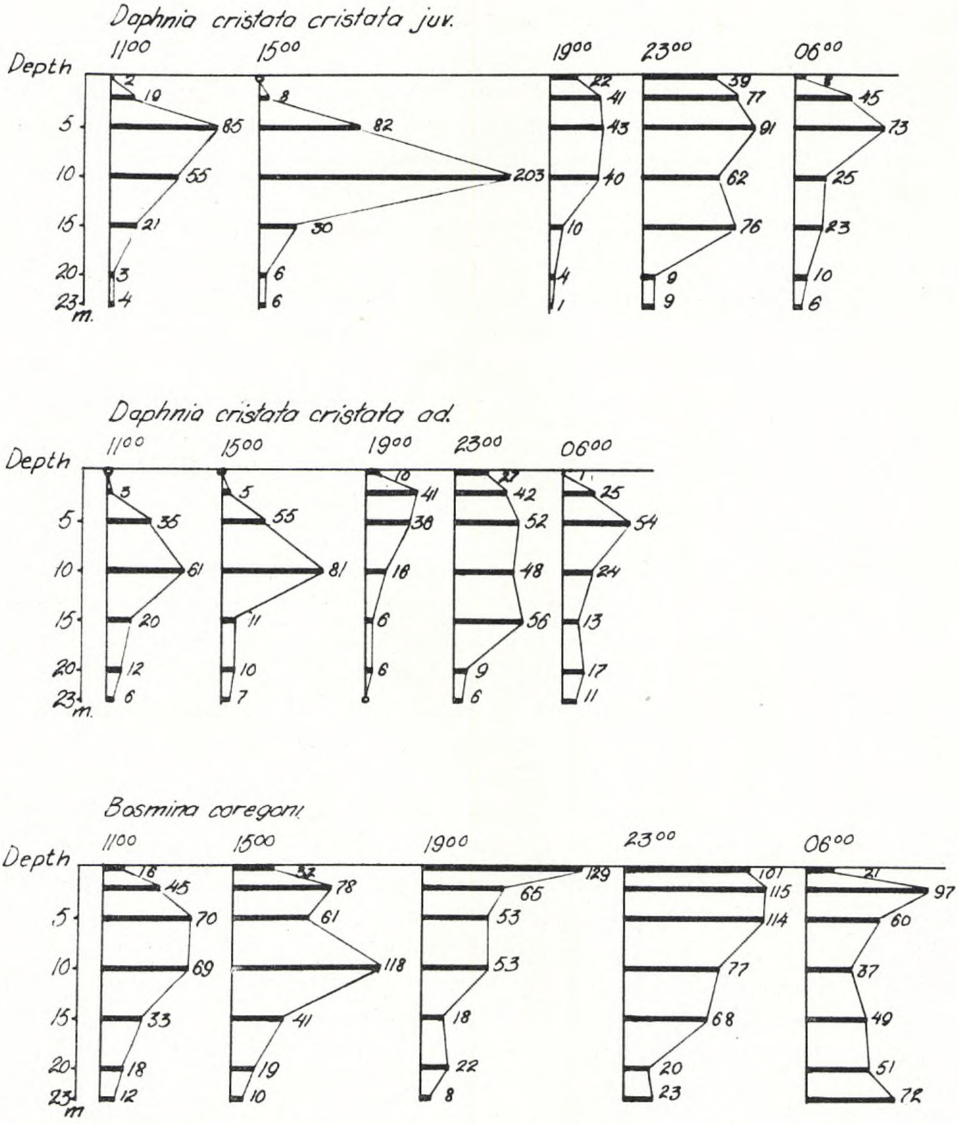


Fig. 7. Vertical distribution of *Daphnia cristata cristata* and *Bosmina coregoni* in Lockne-sjön on August 30th and 31st, 1961. (Individuals/5.3 l.)

uppermost water layers at night. The concentration in these layers seems, however, to be of short duration for before midnight a descent towards deeper water layers has already begun. As the animals are found in large quantities between two and five metres deep at 6 a.m., they may be assumed to have moved upwards again at daybreak. At the same time, however, large numbers are also found close to the bottom. Samples taken at 11 a.m. and

3 p.m. show that in the daytime most animals are found between five and ten metres deep.

It should be noted that in the daytime *Diaptomus graciloides* is generally not found in the same water layer as the other filter feeders, *Daphnia* and *Bosmina,* which may indicate that *D. graciloides* does not compete with the cladocerans for food.

The water volume being on the whole homotherm, it is difficult to state to what extent temperature is a determinating factor on the vertical distribution. The changes that have taken place during the 24 hours may therefore be attributed primarily to changes in the intensity of light.

Results of the present study show that the three species undergo a regular diurnal migration, with all the typical characteristics described by CUSHING (1951).

In his conclusion CUSHING assumes as a probable explanation of the vertical distribution that the animals aggregate in an optimum band of light intensity.

Experiments have shown that the crustaceans move with constant speed toward or away from light and the speed varies with the changes in the light intensity. In complete darkness their activity is probably minimal (CUSHING 1951). According to CUSHING the vertical distribution of the crustaceans at midnight is due to this minimal activity and the ensuing passive sinking of the animals. The results achieved confirm this supposition.

In the morning there are agglomerations of *Bosmina* as well as *Diaptomus* both at 2—5 metres and at the bottom. At dawn the light only penetrates the upper water layers and spreads very slowly to deeper layers. Animals which are deeper down will then remain passive for a longer time and sink still further, while animals in the upper water layers will be affected earlier by light and be found in the layers having the optimum light intensity. A great number of individuals will thus be found fairly deep down during a small part of the morning. The time of the sampling may explain the fact that *Daphnia cristata cristata* has no maximum value close to the bottom. As there are certainly variations between the species as to the speed at which they sink and their sensitivity to light, the species will hardly have an identical distribution at any one hour.

BAINBRIDGE (1961) states the lack of thorough field observations to show the existence or non-existence of midnight sinking and dawn rise. Even if the present investigation is on a small scale, the results seem to indicate that there is a passive sinking at night and an ascent at dawn. In an earlier chapter mention was made of several scientists who have found that the large animals, which can see the sampler, are less numerous in the daytime than at night in samples taken in the same profile. As seen from the diagrams the samples taken at 11 p.m. contain considerably more animals than those taken during the day. Only the nauplii do not show any difference.

The vertical distribution at midnight in the thirteen lakes

The observations of the diurnal migration of *Diaptomus, Daphnia* and *Bosmina* have clearly shown the importance of light for the vertical distribution of the animals in a lake of a homothermal condition. In a stratified lake on the other hand temperature will be of great importance in the distribution of zooplankton whereas light is of less importance. Temperature has both direct and indirect influence on the distribution of plankton. The direct influence is manifested by the fact that each species prefers the water layer having the temperature favourable to that species. What is much more important, however, is the connection between temperature on one hand and density and viscosity of the water on the other hand. The thermocline may act as a barrier for many zooplankters for there is an increase in the density and the viscosity of the water as the temperature falls (see fig. 32—44).

The spring turn-over is still going on in June and the whole water column is homotherm. As the samples were taken at night the greatest concentration of crustaceans was, as expected, found in the upper water layers but there were a great number of animals in the deeper water layers, too. The same vertical distribution was found in Locknesjön at midnight. In July and August the distribution reflects the more or less pronounced stratification of the lakes. The crustaceans are now found in the epilimnion but sometimes there is also small concentration in the metalimnion. Very few individuals are found in the hypolimnion. In many lakes the autumn turn-over has begun in September and the vertical distribution in those lakes is very similar to that of June. There seems, however, to be a greater dispersal of crustaceans at any one hour of the night in September, when the sun sets earlier, than in June (see fig. 37). This observation confirms the opinion that there is a passive sinking of the crustaceans during the dark hours of the night. Some lakes are still stratified in September. The epilimnion then goes further down than in August and there is a corresponding change in the distribution of the animals.

AXELSON (1961 a) has found that the thermocline is an effective boundary below which some rotifers are very few in number whereas the limiting effect of the thermocline on nauplii of *Cyclops* is the reverse. AXELSON draws the conclusion that light is a factor of small importance for the vertical distribution and that food and temperature are the decisive factors. LINDSTRÖM (1952), among other authors, has found a concentration of crustaceans at the thermocline. When studying lakes in Jämtland he has observed that juveniles and males of *Daphnia longispina hyalina* are concentrated at the thermocline. It can therefore hardly be doubted that the thermocline acts as a barrier for the vertical migrations of zooplankton. It has further been observed that the temperature may modify the reactions of crustaceans to light (CUSHING 1951, LINDSTRÖM 1958).

The importance of the direct influence of temperature on the vertical distribution is harder to state. Most species do not seem to be sensitive to the relatively small changes in temperature which are common in a lake (WELCH 1952). The distribution of *Daphnia cristata longiremis* indicates, however, direct influence of the temperature. The few individuals which have been met with of this cold stenothermal animal have always occurred in deep and cold water layers.

Other factors which may influence the vertical distribution are O_2-content and supply of food. As the O_2-content has not been analysed, it is hard to judge the importance of this factor. All the lakes are to be characterized as oligotrophic and there is not likely to be lack of oxygen in the hypolimnion during summer. No more can the importance of food in the vertical distribution of zooplankton be stated with certainty. The crustaceans will generally be most numerous in the layers where there is the greatest supply of food. Still very little is known about the choice of food of the different species. All that can be said at present is that the food factors act at the same time as other regulating factors and with a strength varying from species to species.

The vertical distribution of the crustaceans in the thirteen lakes indicates that light as well as temperature are of importance. During July and August, when the lakes are thermally stratified, the distribution of the crustaceans must to a very large extent be attributed to the temperature. As the difference in temperature between upper and lower water layers decreases, the importance of light as a regulating factor will increase.

A short description is given below of the vertical distribution of the different species on the different sampling occasions. For a closer comparison of the lakes see fig. 32—44.

Copepoda

Diaptomus graciloides. During the spring and autumn turn-over the nauplii are numerous in all water layers from the surface to the bottom but their maximum is generally located in a zone between the surface and 20 metres deep. During the summer stagnation the nauplii are distinctly concentrated in the epilimnion.

No marked difference between the distribution of young and old copepodids could be noticed. They occupy almost the same layers as the nauplii. Most copepodids are found at the surface or at a depth of two metres.

The adults are usually most abundant in the water layers close to the surface. Maximum values are, as a rule, found near the surface and at 2 metres. Males, females and egg-carrying females show the same distribution.

Diaptomus laticeps. The nauplii, which appear during the spring turnover, occur in the whole water column but tend to prefer the upper water layers.

The copepodids have a somewhat irregular distribution. There is usually a maximum in the warm water layers.

Adults usually occur in the upper water layers.

Diaptomus denticornis and *D. laciniatus* have only been found in small numbers but the results indicate that they prefer the layers close to the surface.

Heterocope appendiculata, H. borealis and *H. saliens* have their maxima between the surface and 5 metres. There is no difference between copepodids and adults.

Cyclops scutifer. The nauplii occur in the whole water column and have a fairly irregular distribution. As a rule, the maximum values are found in the epilimnion above the thermocline but sometimes also in the hypolimnion.

The vertical distribution of the copepodids is the same as that of the nauplii.

The adults are uniformly distributed in the whole water column but during the summer stagnation the maximum is found close to the surface. There is no difference between males and females.

Cladocera

Daphnia cristata cristata is common in the upper layers of warm water and often develops maxima at 2 and 5 metres.

Daphnia cristata longiremis. The few individuals occurring have almost exclusively occupied the deeper water layers, the hypolimnion.

Daphnia longispina hyalina has a distribution that indicates a preference for layers close to the surface. The maximum value is often found at 2 or 5 metres. There is a slight tendency for the juveniles to occur in deeper strata than the adults.

Daphnia longispina longispina. To judge from the few individuals occurring in the samples, the vertical distribution coincides with that of *D. longispina hyalina.*

Bosmina coregoni occupies the whole water column from the surface to the bottom. Maxima are found between the surface and 15 m.

Holopedium gibberum is uniformly distributed in the whole water column during the spring and autumn turn-over. But there is a concentration in the warm layers close to the surface even at a time of relatively slight stratification.

Polyphemus pediculus, Bythotrephes longimanus and *Leptodora Kindtii* have only occurred sporadically and therefore it is still difficult to have an exact idea of their vertical distribution. They seem, however, to prefer the upper layers.

It has not been possible to draw any conclusions of the vertical distribution of the remaining crustaceans as they have occurred in too small numbers.

VI. Observations on the annual cycle

As already mentioned the analysis of the samples has been made so as to ascertain the different stages of the annual cycle of each species. Samples from the winter months are missing, but in spite of this the material gives a fairly good idea of the annual cycle of some of the crustaceans that are most common in lakes in northern Sweden.

It should be pointed out once more that nauplii of the genera *Diaptomus* and *Heterocope* have been grouped together as *Centropagidae*. Moreover, very young copepodids of *Heterocope* may be mistaken for copepodids of *Diaptomus* but since they have different annual cycles and *Heterocope,* as a rule, is rare, errors due to this similarity are not likely to arise.

Copepoda

Diaptomus denticornis and *D. laciniatus.* The two species have only occurred in a few lakes and in small numbers. In Borgasjön where they are the only representatives of the genus, they appear in the middle of July, mainly as nauplii, which a month later have developed into old copepodids. The first adults are found at the same time, some females of *D. laciniatus* already carrying egg-sacs. By the middle of September there are only adult *D. denticornis.* The samples contain no nauplii or copepodids and the eggs produced are probably resting eggs which next spring will develop into nauplii. In the other lakes too (Mjölkvattnet, Storsjouten, Torrön) the course of development is similar and adults are not found until August. The first stages of the development, nauplii-copepodids, cannot be distinguished in these lakes since *D. laticeps* co-exists with the species mentioned.

D. denticornis and *D. laciniatus* seem to develop only one generation a year, which is in agreement with Ekman's (1904) results from the Sarek-area.

Diaptomus graciloides. In five of the six lakes, where *D. graciloides* is common, the course of development is strikingly similar during the summer (Övre Björkvattnet, Fjosokken, Rengen, Storuman, Vojmsjön). The differences existing may be due to the species not having reached the same degree of development on the sampling occasions. This is partly due to the geographical situation of the lakes, partly to the time passing between the samplings in the first and the last lake during one and the same month.

Fig. 8 presents the development of *D. graciloides* in Övre Björkvattnet during June—September. At the end of June, nauplii and adults are very numerous and most females are carrying egg-sacs. By the middle of July, the nauplii have for the most part developed into young copepodids which are abundant while the number of nauplii and adults is decreasing. A month later, in the middle of August, the population consists almost exclusively of copepodids, especially old ones. In September the population is composed

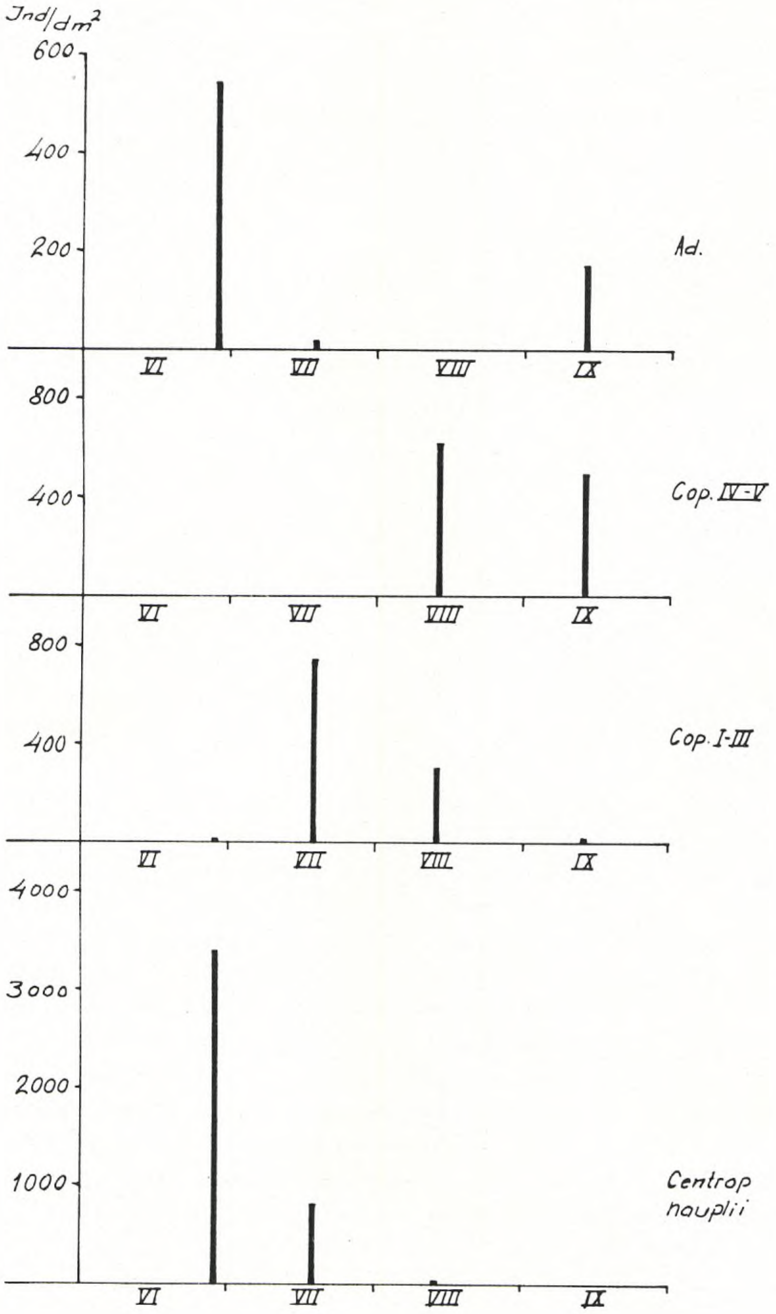


Fig. 8. The development of *Diaptomus graciloides* in Övre Björkvattnet.

by old copepodids and adults but the latter do not yet seem to be sexually mature. No egg-carrying females have been found in Övre Björkvattnet in September.

In the four other lakes the development seems to be more advanced on the first occasions of sampling than in Övre Björkvattnet, for adults are not so numerous at the turn of month June—July. A few adults have been found as late as August. The most interesting difference is constituted by the occurrence in September in Fjosokken, Rengen and Storuman of females carrying spermatophors and egg-sacs. Even if they are not numerous, they may help to explain the annual cycle of *D. graciloides.*

EKMAN, (1904) has found that *D. graciloides* has one generation in the small lakes but two in the large lakes in the north of Sweden. He considers that there are two months after the eggs' being hatched before the females are carrying egg-sacs. RYLOV (1935) states that the species may be mono- or dicyclic and that there may be resting eggs. The results from Övre Björkvattnet well agree with the description of the development of *D. graciloides* in Kultsjön given by AXELSON (1961 a). He has found no egg-carrying females in samples from either September or November. As to the hibernation of *D. graciloides* AXELSON says nothing definite. He suggests that the adults appearing in September hibernate and become fertile only the following spring. As some winter samples contained very few individuals compared to the samples from June, AXELSON draws the conclusion that the adult copepods do not spend the winter in the free water but that most of them stay in the bottom mud or in the water close to the bottom.

To find out how *D. graciloides* passes the winter in lakes in northern Sweden, more samples from late autumn, spring and even winter would be required. The results seem to indicate that the development in Övre Björkvattnet is delayed compared to that of the other lakes which is perhaps owing to the late ice-break in Övre Björkvattnet (LINDSTRÖM, 1958). The reproduction of *D. graciloides* might then be expected to fall in the end of September or in October. AXELSON has no samples from October but from November, when the population in Kultsjön consists only of adults. As *D. graciloides* has had an identical development in the two lakes earlier in the summer, the development may be supposed to follow the same course in the two lakes in late autumn, too. The animals probably hibernate as adults which are not yet sexually mature. Thus the results from Övre Björkvattnet seem to confirm AXELSON's conclusions.

The occurrence in September of a small number of egg-carrying females in the other lakes may suggest that in these lakes *D. graciloides* passes the winter in another stage of development. The insufficient material allows no definite conclusions. The population is possibly divided into two fractions, as is the case of other copepods in lakes in northern Sweden (LINDSTRÖM 1952, 1958, AXELSON 1961 b). The population observed in Övre Björkvattnet would

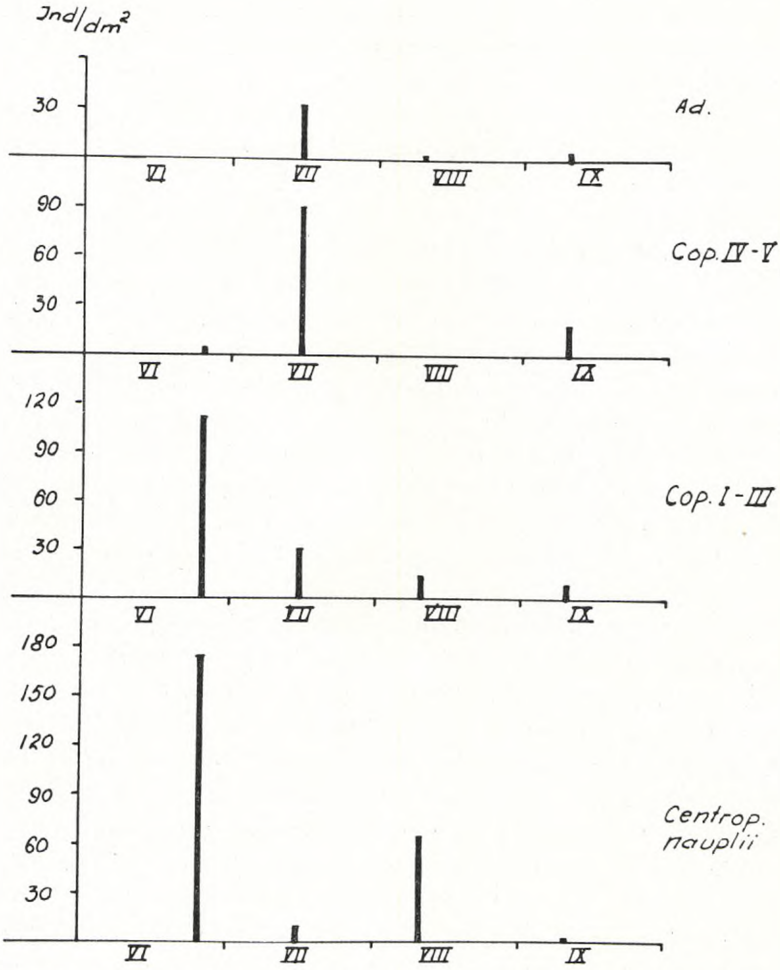


Fig. 9. The development of *Diaptomus graciloides* in Storjuktan.

then correspond to one of these fractions and would consequently hibernate as adult individuals. The second fraction would comprise the individuals which reproduce in autumn and hibernate as resting eggs or nauplii or copepodids. There are no definite proofs that such a dualism exists.

To judge from the material present there seem to be two fractions in *Diaptomus laticeps* and *Cyclops scutifer*. It is still impossible to establish what these fractions represent from genetical taxonomical viewpoints.

In the lakes described above, *D. graciloides* has had one generation a year but the results from Storjuktan would point to the existence of two generations during the ice-free months (Fig. 9). At the end of June there are almost exclusively nauplii and young copepodids, which have developed into old copepodids or adults by the middle of July. At the beginning of August old copepodids as well as adults are very rare while nauplii and young copepodids are again abundant. In September copepodids and adults have taken their place. In July and September there is the greatest number of egg-carrying females. The decrease in the number of nauplii in July and the heavy increase in August may signify that the nauplii found in August belong to a second generation.

As the lake is covered with ice as early as the end of October (Table 2) *D. graciloides* probably does not hibernate in the same stage of development in Storjuktan as in the lakes described earlier. The eggs formed in autumn are probably resting eggs which are hatched only the following spring. This is confirmed by the composition of the population in June. The nauplii and young copepodids occur in great numbers but no adults are found from which the nauplii might derive.

Diaptomus laticeps. Just as the former species, *D. laticeps* shows a course of development that is different in different lakes and in this respect the lakes may be divided into two groups, Ottsjön, Storsjouten, Stora Mjölkvattnet, Rengen on one hand and Kvarnbergsvattnet, Torrön and Övre Björkvattnet on the other.

To illustrate the differences of the annual cycle, Ottsjön and Kvarnbergsvattnet have been chosen. In the other lakes there are other diaptomids, too, and as the nauplii and copepodids have not been identified to species, there is greater difficulty in getting an exact idea of the development. In Ottsjön the population is made up of old copepodids and adults during the latter half of June. Nauplii and young copepodids occur only in small numbers and have disappeared completely by the beginning of July when the old copepodids have become adults. At the beginning of August the population consists only of adults, some of which are egg-carrying females. A month later both males and females occur but now in considerably smaller numbers. The eggs formed in August—September are resting eggs which are hatched the following spring. LINDSTRÖM (1952) has found nauplii in winter samples (February—March) from Ottsjön and copepodids at the ice-break, which indicates that eggs are hatched already during the winter months. The main part of the eggs are, however, hatched during the time of the ice-break, when he has found an increase in the number of nauplii.

In 1957 the ice-break took place on May 27th in Ottsjön. In the samples from June 20th, less than a month later, the number of nauplii and young copepodids was very small and the population was made up of old copepodids and adults. The first stages of development were rapidly passed but then it was not until the beginning of August that the first egg-carrying females were observed.

In Storsjouten, Stora Mjölkvattnet and Rengen the number of adult *D. laticeps* is very small. Egg-carrying females appear in July and August and the remaining phases of the development will be very similar to that in Ottsjön.

In Kvarnbergsvattnet the population is composed of nauplii and adults on July 4th and a great number of egg-carrying females can be observed. On July 20th the situation is much the same. In the middle of August there is a distinct decrease in the number of nauplii and adults at the same time as the copepodids show a heavy increase. On September 15th the population consists for the main part of old copepodids.

The nauplii occurring in July hardly derive from resting eggs but may be the offspring of the animals found in June and July. In September these nauplii have developed into old copepodids which probably hibernate as such and became adults the following spring when reproduction takes place. To judge from the results from Torrön and Övre Björkvattnet *D. laticeps* has a similar annual cycle in these lakes.

In Överuman the annual cycle of *D. laticeps* seems to be more complicated. Unfortunately, samples have been procured only from the months July—September. In the middle of July all stages of development from nauplii to egg-carrying females are represented. The nauplii are numerically dominating. A month later the females have disappeared and the nauplii have been replaced by young copepodids. In September there are hardly any nauplii left but egg-carrying females appear again. The development shows features characteristic of the annual cycle such as it is found in Ottsjön as well as in Kvarnbergsvattnet. The only explanation that can be advanced at present as to the course of development in *D. laticeps* is the population's being divided into two fractions. One fraction would then have its period of reproduction in spring, the other in autumn. LINDSTRÖM (1958) has observed the same phenomenon in some lakes in Jämtland.

The number of copepodids and adults found in September is strikingly lower than the number of nauplii and copepodids found in August. This applies not only to Överuman but also to Kvarnbergsvattnet. The heavy reduction of the population may be caused by the deterioration in the environment followed by a rise in mortality or, more likely by the old copepodids leaving the free water to pass the winter months on the bottom or close to it, thus avoiding the plankton sampler. As mentioned earlier, AXELSON has found that *D. graciloides* probably passes winter on or near the bottom and not in the free water. It remains to find out if the same thing is true also about *D. laticeps* and if so, the reduction in September would find its explanation. It seems incredible that such a marked decrease in the population, taking place as early as September, could be explained only by losses through the outflow.

Heterocope appendiculata, H. borealis and *H. saliens.* The development from nauplii to adults is more rapid in these species than in the other copepods studied, and the development of the three species seems to follow the same course. As a rule the population is composed of copepodids in July and as early as August the first adults are found, occurring in the samples as late as September. In Storjuktan and Storsjouten adult specimens have, however, appeared already in July. The eggs are resting eggs.

In this connection, the following observation can be mentioned. In September all the adults of *H. saliens* were covered by suctorians in Borgasjön and Kvarnbergsvattnet. That was also the case in Storsjouten in August. On the contrary, only very few individuals were affected in Övre Björkvattnet in September. All the time only adults were concerned; no copepodids were affected, and this may be explained by the fact that the rapid growth brings about such frequent moultings that the suctorians never have time to develop. The age of the copepod population may also be of some consequence as the resistance of the copepods is probably gradually reduced.

Cyclops scutifer. This species is very common in the north of Sweden and in many lakes it is often the only representative of the genus. It occurs in all the lakes dealt with in this paper. The results indicate, however, that the annual cycle of *C. scutifer* is not identical in these lakes but that during summer the development varies in different lakes. According to EKMAN (1904) nauplii represent *C. scutifer* in the small mountain lakes at ice-break. Some four weeks later, the nauplii have become adults and the females are carrying egg-sacs. This generation is followed by another the same year. In the large lakes, the situation is more complicated. The same author states that the population contains nauplii, copepodids and even a few adults at the ice-break. LINDSTRÖM (1952, 1958) who has studied the annual cycle of copepods in lakes in Jämtland, has found that the population of *C. scutifer* consists of two fractions with different annual cycles. The same dualism has been found in Ransaren by AXELSON (1961 b).

The results of the present investigation will agree with those achieved by LINDSTRÖM. In the following description of the annual cycle the fractions will be denoted A and B in accordance with LINDSTRÖM's terminology. In five of the thirteen lakes the population of *C. scutifer* has a development that indicates a division into two fractions. The development such as it is found in Ottsjön may be said to be representative in this respect.

During the latter part of June the population is mainly made up by copepodids and adult cyclopoids (Fig. 10). A great many females are carrying egg-sacs. Three weeks later old copepodids have replaced the young copepodids and are very abundant. Adults still occur in great numbers. An increase in the number of nauplii is noted. At the beginning of August the number of adults is small as well as that of young copepodids. Nauplii and old copepodids make up the *Cyclops*-population and in September they have developed into young copepodids and adult *Cyclops* respectively. The nauplii which derive from the adults in July have increased in number.

The composition of the population in June and September clearly shows that in Ottsjön there are two fractions having different annual cycles. Fraction A comprises the young copepodids occurring at the end of June. They

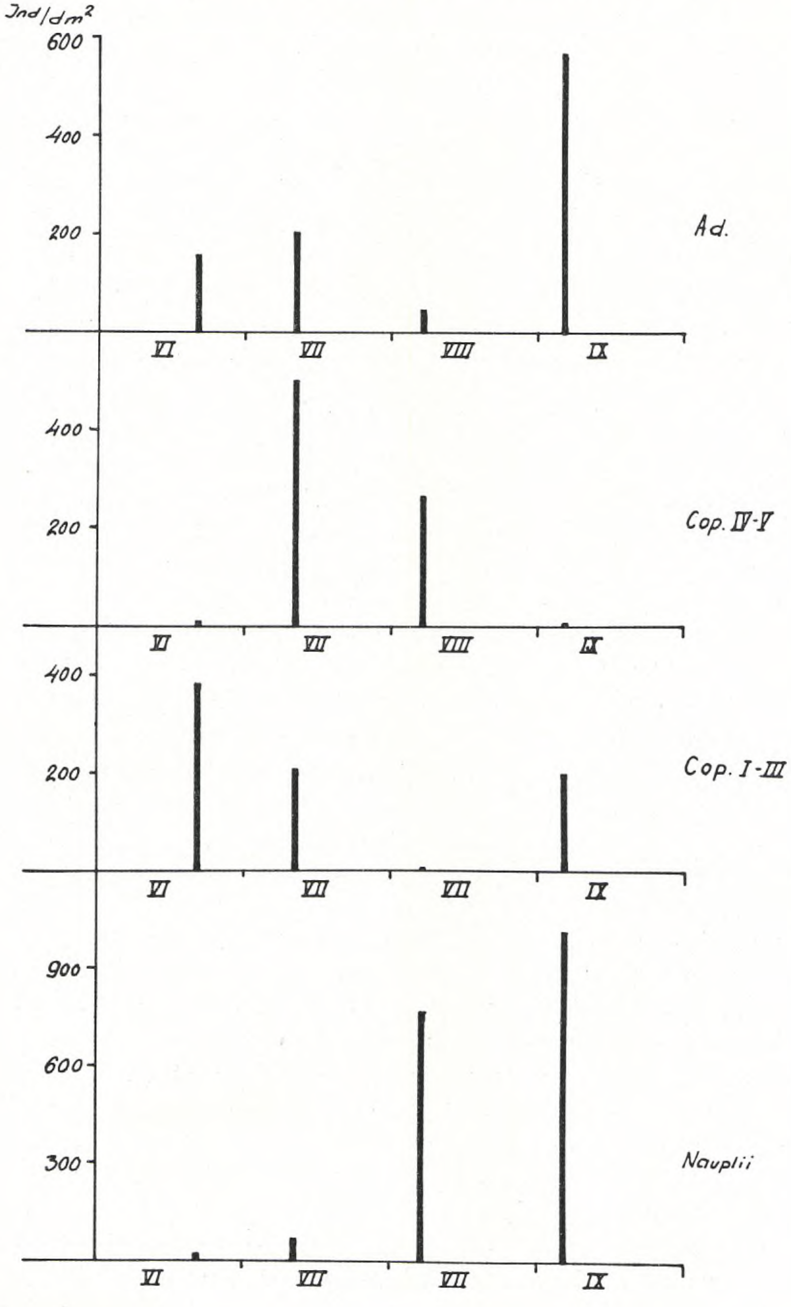


Fig. 10. The development of *Cyclops scutifer* in Ottsjön.

become adults and reproduce during autumn. The second fraction, B, is composed of the adults appearing in spring and early summer. Their offspring passes the summer as nauplii which develop into young copepodids towards the end of the summer. They pass the winter as young or old copepodids.

LINDSTRÖM (1958) states in his paper that this fraction originates from a spring pulse of nauplii and young copepodids, but makes a reservation as to the origin of the nauplii. AXELSON (1961 a) has in some winter samples found nauplii in great numbers but no adults and is of opinion that the nauplii originate from egg-carrying females in August.

Several authors (among others DIETRICH 1915, WALTHER 1922, COKER 1933) have proved that the development is more rapid at high temperatures provided that the food is sufficient. During the winter months when temperature and food supply are at their lowest, the development of the nauplii will more or less come to a standstill. Fraction A therefore probably passes the winter as nauplii, fraction B as young or old copepodids.

The *Cyclops*-population has proved to be divided into two fractions also in Borgasjön, Kvarnbergsvattnet, Torrön and Vojmsjön. This dualism is not equally obvious in all the lakes. As all the individuals of a fraction do not have the same rate of development, adults of the B-fraction may occur as late as August, when adults of the A-fraction may also be expected to appear. It is not established that a genetic difference between the two fractions should develop in view of the tendency to fusion of the fractions. AXELSON (1961 b) has found differences in body length, but no other morphological differences have been noted between the two fractions. As has been said above, nothing can be said with certainty as to the genetical and taxonomical importance of the dualism.

The development of the *Cyclops*-population in Fjosokken and Storuman shows some deviations from the description given above and corresponds rather to fraction A in Ottsjön. A few adults have been observed at the end of June and in July but their small number and the lack of egg-carrying females make one believe that it is only a matter of individuals having passed the different stages of development more rapidly than the rest of the population. There is thus probably no dualism in Fjosokken and Storuman but the whole population has an annual cycle which most nearly resembles fraction A of the lakes earlier mentioned.

To judge from the results from Övre Björkvattnet, Rengen, Storsjouten (Fig. 11) and Överuman the existence of a dualism in the *Cyclops*-population in these lakes may also be questioned. *C. scutifer* is found to have a period of reproduction in spring and early summer, and this is reminiscent of the development of the B-fraction in Ottsjön. The autumn samples contained, nevertheless, a small number of egg-carrying females which might indicate that a small part of the population has an annual cycle similar to

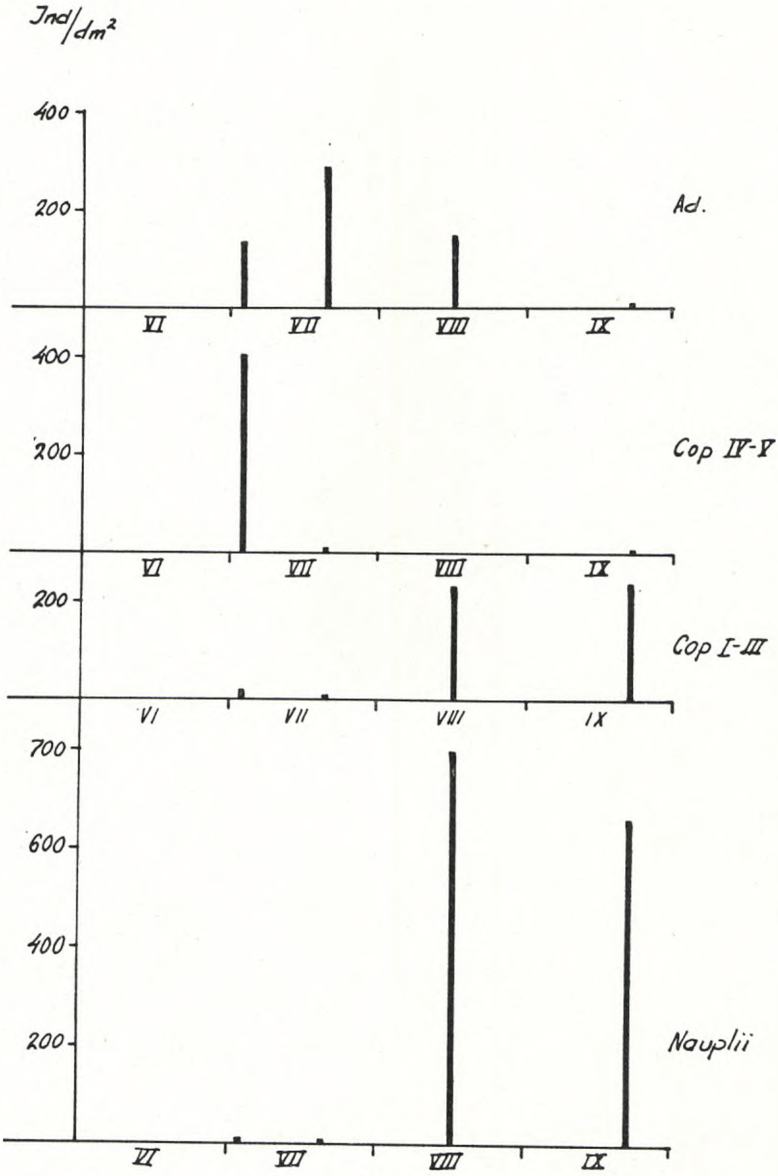


Fig. 11. The development of *Cyclops scutifer* in Storsjouten.

that of fraction A. Considering, however, the small number, the individuals concerned may have developed more rapidly than usual. Moreover, individuals that are adults in June may live until August (LINDSTRÖM 1952). However that may be, the *Cyclops*-population resembles the B-fraction of Ottsjön and if there is a dualism at all, the fraction A is not very prominent.

The results from Stora Mjölkvattnet differ from that of the lakes mentioned above in one respect. Old copepodids abound in samples taken on September 17th. They possibly reach sexual maturity and reproduce late in autumn. In such case there is also an A-fraction, which seems likely if the composition of the population during the summer is borne in mind. The material is, however, insufficient for any conclusions about the annual cycle of this lake to be drawn.

It has not been possible to ascertain the annual cycle of *C. scutifer* in Storjuktan. No egg-carrying females have occurred. The adults have been *C. scutifer* but some copepodids may belong to another species.

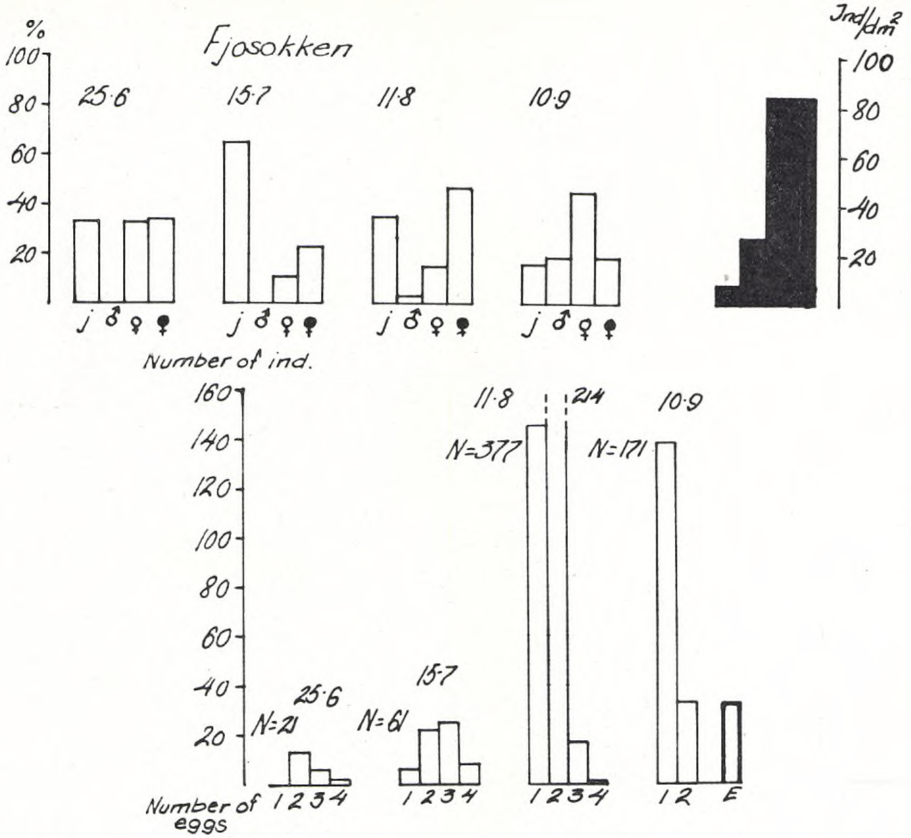
Cladocera

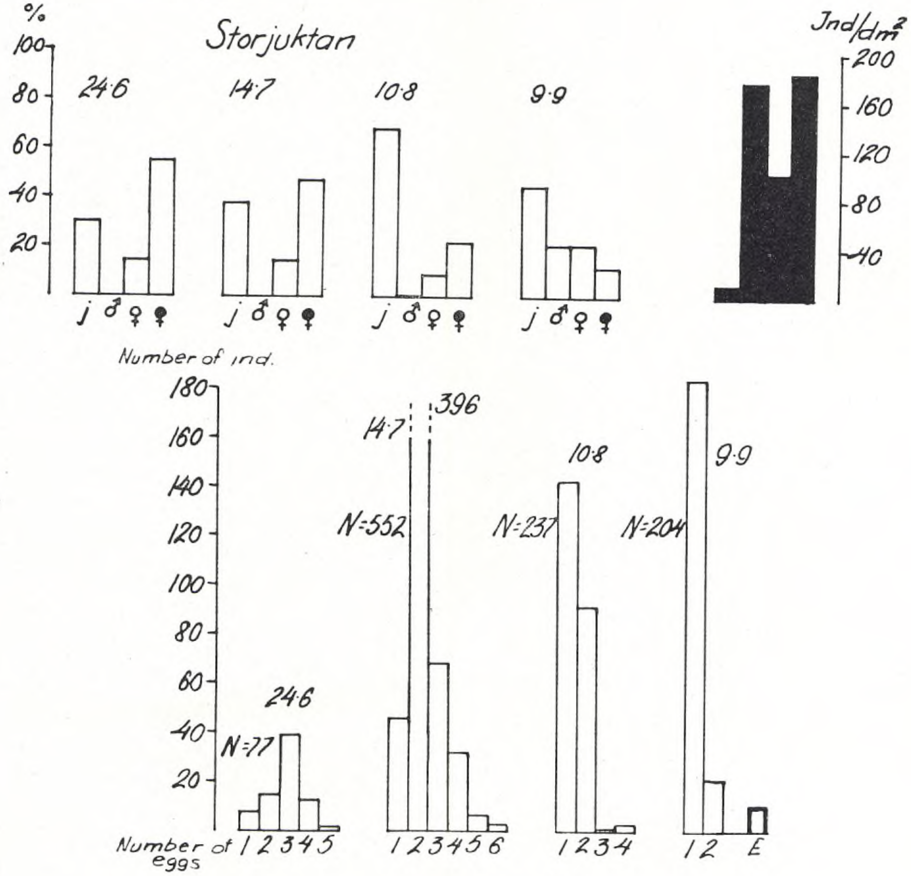
Daphnia cristata cristata. The life cycle in summer is strikingly similar in the four lakes, where *D. cristata cristata* is very common. The development starts earlier in the shallow lakes Fjosokken and Storjuktan than in the large and deep lakes Storuman and Vojmsjön, which is probably accounted for by the slow rise in water temperature of the two latter lakes. By the end of June the number of individuals is very small (Fig. 12—13) and the animals are, for the main part, not yet adult. In Fjosokken and Storjuktan at this time some females are even carrying eggs. As many as five eggs have been observed, but as a rule the females have two or three in the brood chamber. At this time, the population is probably made up of individuals originating from ephippia.

In the middle of July the density of individuals in Storuman and Vojmsjön is about the same as at the end of June but some 20 % of the population consists of egg-carrying females. In the two other lakes and especially in Storjuktan the number of individuals, mainly composed of juveniles and egg-carrying females, has increased strongly. After the ice-break, the water of Storjuktan is warmed very quickly and consequently not only are the ephippia hatched earlier but development as a whole is hastened. Juveniles and egg-carrying females dominate in the samples from August. The females have one or two eggs in the brood-chamber. More than two eggs are rarely found during this month.

A month later, at the beginning of September, the number of individuals is at its greatest. Males make up about 20 % of the population and the percentage of juveniles has decreased compared to what was usual in July. The egg-carrying females form but a little part of the population and in no lake do they exceed 10 %. As a maximum they have two eggs but most of them have only one. Some of the females have developed an ephippium. In Storjuktan about 5 % of the egg-carrying females have a more or less well devel-

Fig. 12. The composition of the population of *Daphnia cristata cristata* in Fjosokken and Storjuktan. In black the number of individuals/dm^2. The number of eggs found in the brood chambers. j=juveniles, ♀=egg-carrying females, E=ephippium.


Fjosokken
%
100
80
60
40
20
25·6
15·7
11·8
10·9
j ♂ ♀ ♀
Jnd/dm²
100
80
60
40
20
Number of ind.
160
140
120
100
80
60
40
20
25·6
N=21
15·7
N=61
11·8
21·4
N=377
10·9
N=171
Number of eggs
1 2 3 4
1 2 3 4
1 2 3 4
1 2
E


Storjuktan
%
100
80
60
40
20
24·6
14·7
10·8
9·9
j ♂ ♀ ♀
Jnd/dm²
200
160
120
80
40
Number of ind.
180
160
140
120
100
80
60
40
20
24·6
N=77
14·7
39·6
N=552
10·8
N=237
9·9
N=204
Number of eggs
1 2 3 4 5
1 2 3 4 5 6
1 2 3 4
1 2
E

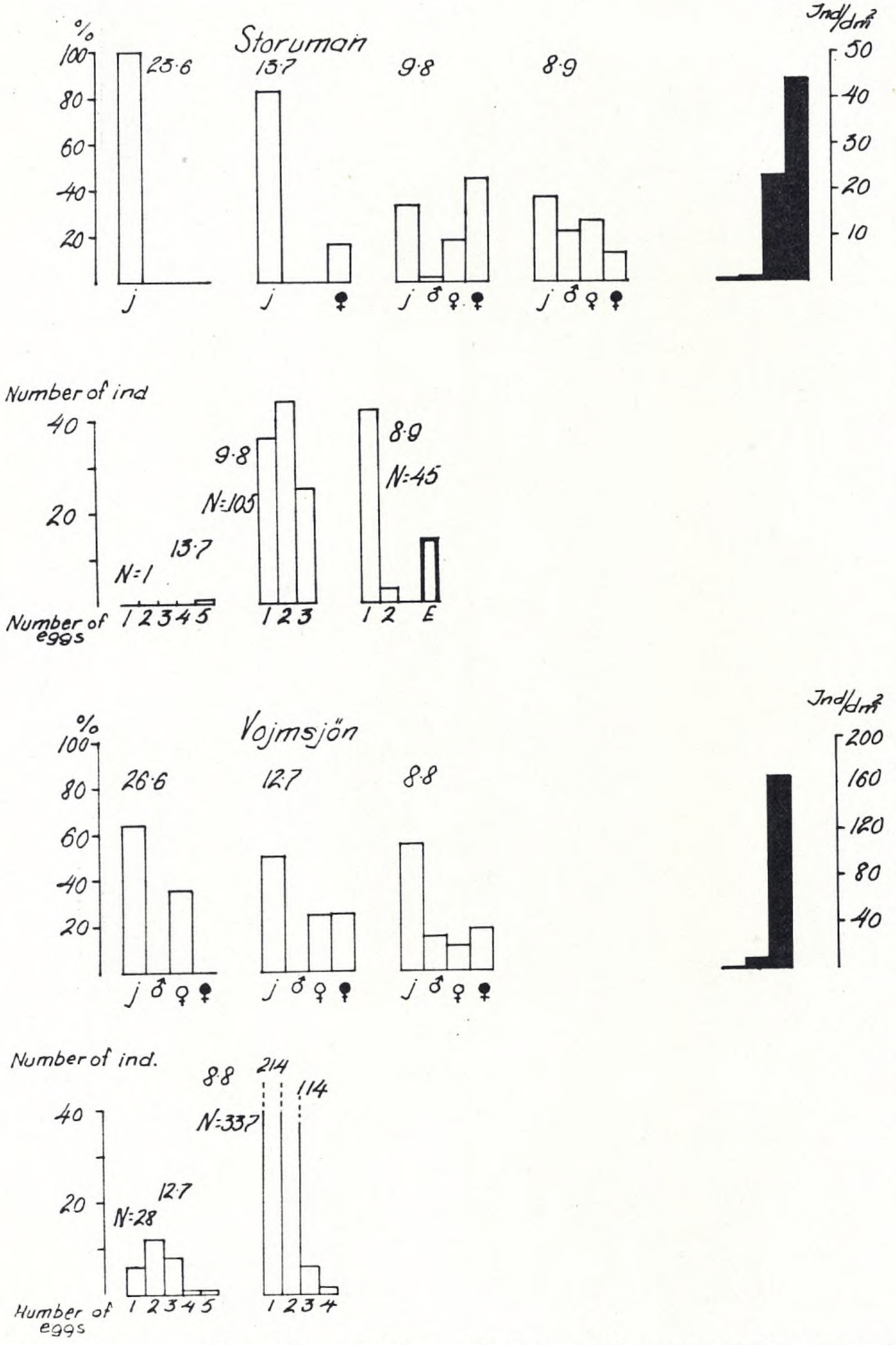


Fig. 13. The composition of the population of *Daphnia cristata cristata* in Storuman and Vojmsjön. In black the number of individuals/dm². The number of eggs found in the brood chambers. j=juveniles, ♀ =egg-carrying females, E=ephippium.

oped ephippium. In Fjosokken the corresponding percentage is 19 and in Storuman 31. No samples were taken in Vojmsjön in September. As a rule *D. cristata cristata* has fewer eggs than *D. longispina hyalina.*

As the cladocerans reproduce parthenogenetically during summer and as there are several parthenogenetic generations following each other, the number of individuals will increase very rapidly. In Storjuktan there is in three weeks an increase of the population from 10 individuals/dm^2 to 180 individuals/dm^2. In Storuman and Vojmsjön there is hardly any change in the size of the population between the samplings of June and July, and as has already been stated the results indicate that in these two lakes the development of *D. cristata cristata* is delayed compared to the smaller and shallower lakes Fjosokken and Storjuktan. The ice-break takes place at about the same time in the four lakes (Tab. 2). During June, however, the water of the lakes is not warmed equally fast. When the June samples were taken, at the end of the month, with the spring turn-over still going on, Storjuktan had a water temperature of about 9°C, Vojmsjön 4.5°C, Fjosokken 8°C and Storuman 6°C. Also during the samplings of July there were great differences in temperature between Fjosokken and Storjuktan on the one hand and Storuman and Vojmsjön on the other. There seems to be a marked relationship between temperature and the growth of the *Daphnia*-population in the lakes. At the end of June, *D. c. cristata* is very rare in all the lakes and is represented mainly by young individuals. Only in Fjosokken and Storjuktan are there egg-carrying females. Three weeks later, in the middle of July, there is a heavy increase in the population, especially in Storjuktan and Fjosokken, while the number of individuals is fairly unchanged in Storuman and Vojmsjön, where a greater number of individuals can be noted first only at the beginning of August. The temperature conditions of the lake will thus influence not only the annual cycle of the species but also the size of the population. If the annual cycle is delayed in spring, the growth of the population is checked by the fact that fewer parthenogenetic generations have the possibility to develop before the end of the short summer. This fact must not be overlooked when comparisons are made between the populations of different lakes. In all the lakes the sexual reproduction period falls at about the same time. Males occur at the beginning of August and a month later a great deal of the adult females are carrying ephippia.

According to RYLOV (1935), *D. c. cristata* is an eurythermal species. In an earlier chapter it has been stated that it only occurs in lakes containing other eurythermal species and is lacking in mountain lakes with cold stenothermal animals. When studying the vertical distribution of the species, FREIDENFELT (1913) has found that it prefers the layers having a temperature above 8—9°C. As to the temperature requirements of the species the vertical distribution in the lakes of northern Sweden gives no direct indications, as the samples are taken at night, when most animals are found in the upper water layers. On the other hand, a comparison of the four lakes shows that egg-carrying females occur only when the greatest part of the water column has reached a temperature of about 8°C. The appearance of adult females with parthenogenetic eggs only at the temperature of 8—9°C shows that this temperature is of the greatest importance for the propagative phase of the animals. Laboratory experiments might give further information as to the direct and indirect influence of temperature on the biology of *D. c. cristata.*

Daphnia cristata longiremis. This cladoceran has only been found in very small numbers in four lakes. As can be seen from the diagrams of the vertical distribution (Fig. 33, 38, 40, 42) it appears almost exclusively in the deep and cold parts of the lakes which have a temperature below 9°C. This is well in accordance with the observations made by FREIDENFELT (1913), who established that *D. c. longiremis* is a cold stenothermal animal as distinguished from *D. c. cristata.* During the summer months there are juveniles as well as adult females and the females are carrying only one or two eggs in their brood chambers. No males or females with ephippium have been observed.

Daphnia longispina hyalina (Fig. 14—15). At the end of June and the beginning of July juveniles and adult females make up the population. The majority of the females are carrying eggs and they have 3—7 eggs in their brood chambers. There is a heavy increase in the population of all the lakes in July and during the latter part of the month the population is to some 60 % made up of juveniles. At the same time there is a tendency among the females to carry fewer eggs. The first males are observed in Övre Björkvattnet, Borgasjön and Kvarnbergsvattnet. In the two latter lakes as well as in Rengen and Storsjouten the number of individuals making up the population is just then at its highest. The number then gradually decreases during August and September. With the exception of Övre Björkvattnet and Överuman and to some extent Torrön, *D. longispina hyalina* decreases in number in August. The males grow more numerous during this month and the females generally carry no more than two eggs. In Övre Björkvattnet, Borgasjön and Kvarnbergsvattnet, where males appeared as early as July, most females have developed ephippia. In September, Ottsjön and Torrön have the greatest density of individuals while the other lakes have a decreasing population of *D. longispina hyalina.* The part of the population made up of juveniles grows smaller owing to the fact that the reproduction is sexual and ephippia with resting eggs are produced. A considerable part of the egg-carrying females are also carrying ephippium.

From a comparison between the annual cycle of *D. longispina hyalina* and that of *D. cristata cristata* it may be concluded that the two species differ as far as their requirements as to temperature are concerned. To judge from the results the parthenogenetic reproduction of *D. longispina hyalina* starts earlier in spring and at a lower water temperature than is the case with

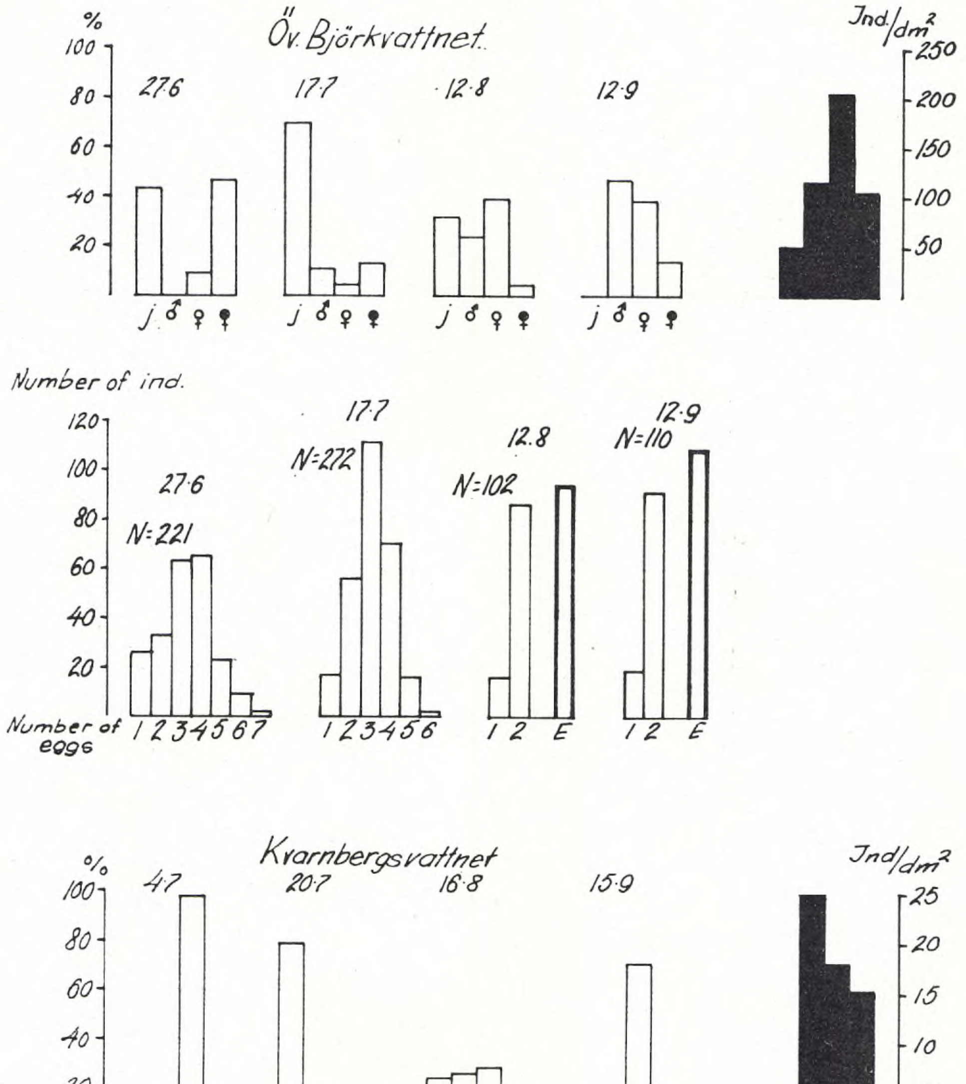


Fig. 14. The composition of the population of *Daphnia longispina hyalina* in Övre Björkvattnet and Kvarnbergsvattnet. In black the number of individuals/dm². The number of eggs found in the brood chambers, j=juveniles, ♀=egg-carrying females, E=ephippium.

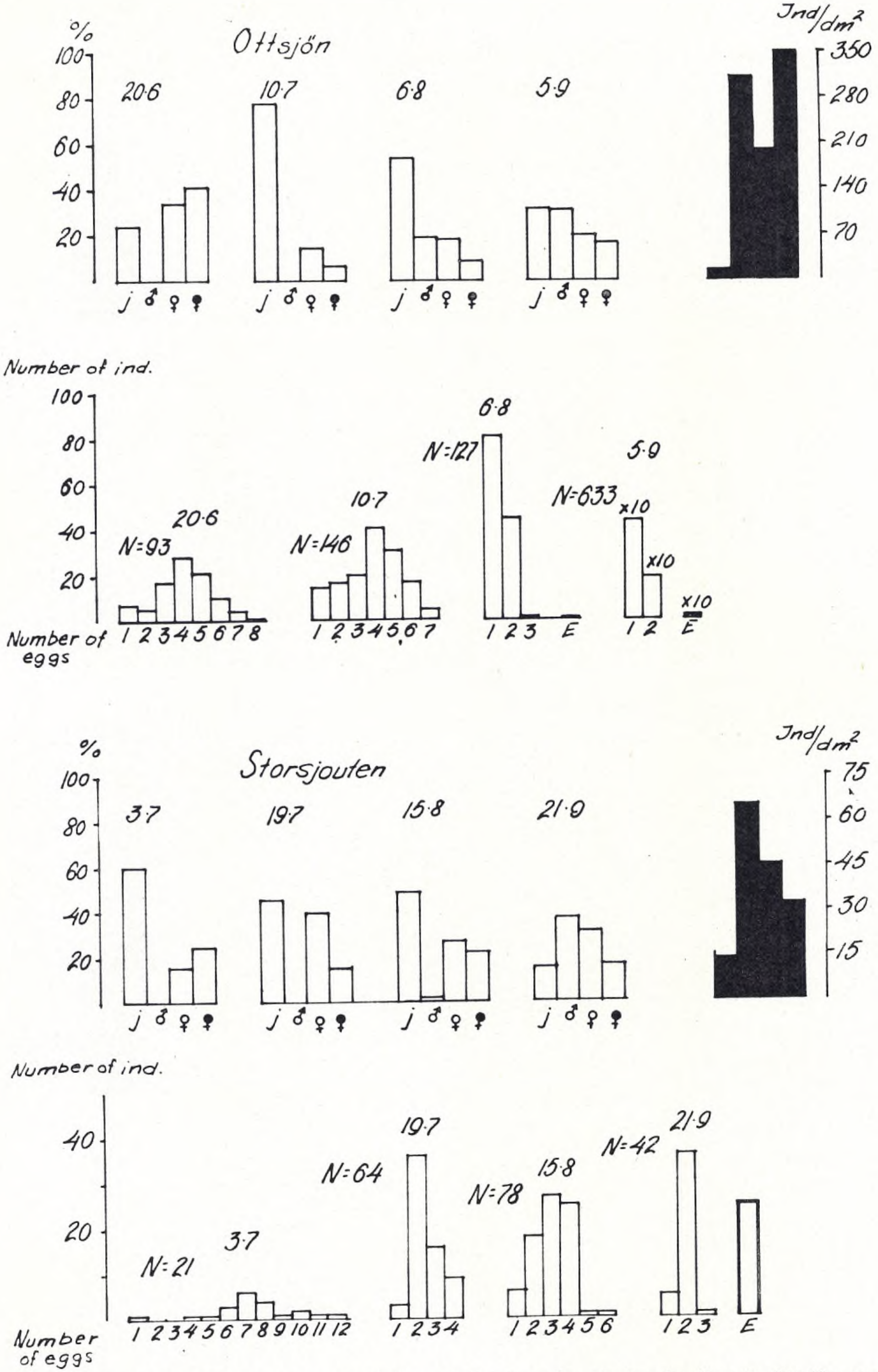


Fig. 15. The composition of the population of *Daphnia longispina hyalina* in Ottsjön and Storsjouten. In black the number of individuals/dm^2. The number of eggs found in the brood chambers. j=juveniles, ♀ =egg-carrying females, E=ephippium.

D. cristata cristata. In Övre Björkvattnet, for example, there occurs about the same number of egg-carrying females as there are juveniles three weeks after the ice-break at a temperature of only 5—6°C. The resting eggs of *D. longispina hyalina* are probably hatched earlier than those of *D. cristata cristata* but apart from this and whatever factor directly affects the hatching of the resting eggs (VOLLMER 1912, WOOD-BANTA 1937, COMITA 1956) it is clear that the parthenogenetic reproduction of *D. longispina hyalina* takes place at a lower water temperature than that of *D. cristata cristata.* The result is that a population of *D. longispina hyalina* grows more rapidly during the early summer than a population of *D. cristata cristata.*

Daphnia longispina longispina. In the lakes where it has been found, Rengen and Torrön, this cladoceran has been represented by the variety *cavifrons* SARS. At the end of June and beginning of July the population mainly consisted of not yet adult animals. Males occur at the end of July and in Torrön a month later most females are carrying ephippia. In Rengen most males disappear in August and during this month there is a slight increase in the population. In both lakes in August and September the females never carry more than two eggs in their brood chambers.

Bosmina coregoni. This is the most common and the most numerous cladoceran, which occurs in all the lakes throughout summer. The development starts early in spring. LINDSTRÖM (1952) has found that in Ottsjön all the individuals of *Bosmina* were carrying eggs or embryos in their brood chambers immediately after the ice-break, in 1950.

At the end of June when the first samples were taken, the composition of the population is fairly similar in all lakes (see diagrams of the vertical distribution). Egg-carrying as well as not egg-carrying animals are found. The latter are dominating and a great deal of them are not yet adult. In July there is a heavy increase in the number of individuals and in five lakes (Ottsjön, Rengen, Storjuktan, Storsjouten, Vojmsjön) the highest values of the summer are then noted. At the same time the greatest number of females carrying eggs is also noted in many lakes while in others this maximum value is found only in August or September.

LINDSTRÖM (1952) states on the contrary that in Ottsjön the egg-carrying females decreased in number in June, disappeared completely in July and appeared again in August in small numbers. According to LINDSTRÖM, *Bosmina coregoni* thus has two periods of reproduction, the first in connection with the ice-break, the second during late summer. Egg-carrying females have been found in all the series of samples from the thirteen lakes. In a paper (1958) LINDSTRÖM has stated that there is a delay in the annual cycle of the crustaceans the years when the ice-break is late. That was the case in 1957 (Table 2), while the ice-break was relatively early in Ottsjön in 1950, the year when LINDSTRÖM collected his samples. This probably accounts for the differences between the results. As regards the annual cycle of *Bosmina* *coregoni* LINDSTRÖM (1958) states, without going into details, that the population reaches its maximum density late in 1957.

It has already been said that in 1957 the *Bosmina* population contained a relatively large number of egg-carrying females in July. Probably there is no interval between the two reproduction periods of *Bosmina* during a year with late ice-break but instead there is an overlapping shown by the occurrence of Bosmina throughout the summer. In some lakes there is a small increase in the number of egg-carrying females in July and an occasional decrease in August while in other lakes there is no decrease until September. This indicates that *Bosmina* may have a reproduction period also during late summer.

Males were found in August and occur during September in all lakes except Ottsjön where, on September 5th, no males could be observed. Further indication about the composition of the population on the different occasions of sampling may be drawn from the diagrams showing the vertical distribution.

As mentioned above, *Bosmina coregoni* increases heavily in number during early summer and in five lakes the population reaches its maximum density in July (Fig. 18). Among these lakes, Ottsjön and Storsjouten have a decrease in population in August and an increase in September. In seven lakes *Bosmina* shows the greatest density of individuals in August but even in September the number of individuals is high in these lakes. In Stora Mjölkvattnet the population reaches its maximum value only in September.

AXELSON (1961 a) has not been able to establish the existence of a sexual reproduction period of *Bosmina coregoni* in Ransaren and Kultsjön. He supposes that the annual cycle is acyclic and the population probably hibernates with a small number of parthenogenetic animals in the littoral zone. The results of the present investigation indicate, however, that *Bosmina coregoni* has a sexual reproduction period. Unfortunately there are no samples from October but it seems probable that the males become more and more numerous during this month. In September many females were carrying only one or two eggs, probably resting eggs. The fact that the males occur in autumn need not mean that the whole population hibernates as resting eggs. As winter samples (LINDSTRÖM 1952, AXELSON 1961 a) have shown that even after the formation of the ice-cover there are *Bosmina* females in the free water, part of the population may evidently hibernate as parthenogenetic females.

Holopedium gibberum. Like the preceding species *Holopedium gibberum* was also common in all the lakes. It should be noted that, as regards this species, the material has been treated differently from that of the species already dealt with insomuch as a division has been made only into egg-carrying and not egg-carrying animals.

In the lakes studied the individuals are mainly not yet adult at the turn of the month June—July (see diagrams of the vertical distribution). The adults have not yet eggs in their brood chambers. The population has already reached its maximal density in Fjosokken, Rengen and Storsjouten (Fig. 18) but in most lakes the maximum is found only about the middle of July. The population then consists to a great part of females carrying a varying number of eggs. During August and September *H. gibberum* grows less numerous in all the lakes at the same time as the first males are observed. Borgasjön, Storuman, and Överuman where the species is most numerous in August, are exceptions. There are fewer and fewer egg-carrying females during the latter part of the summer and they have fewer eggs in their brood chambers. In the September samples from Fjosokken, *H. gibberum* is completely lacking.

When studying *Holopedium gibberum* in the south of Sweden, FREIDENFELT (1920) has found that it takes a remarkably long time before the individuals, originating from the resting eggs, start reproducing themselves. He observed the first juveniles as early as the middle of April but only at the end of May did the parthenogenetic reproduction start. As the breaking up of the ice takes place considerably later in the lakes in northern Sweden, one may assume that the individuals found at the end of June come from resting eggs. Their period of reproduction then falls in July—August.

In his lakes in southern Sweden, FREIDENFELT (1920) has found the same pattern of development as that described for lakes in northern Sweden, characterized by a maximal density of individuals in July followed by a marked decrease during the following months. The lakes in northern Sweden show, however, a retardment of the annual cycle. FREIDENFELT finds that *H. gibberum* again increases in number during the autumn and the population has once more a maximum value in October. In January the species only occurs sporadically in the samples. Whether a population in a lake in northern Sweden follows the same course of development cannot be concluded, as samples are lacking from late autumn.

For the present it may be assumed that the hard climate of northern Sweden has shortened the annual cycle of *H. gibberum* as is the case with many other cladocerans, so that the population has only one maximum value of density during the year (EKMAN 1904).

The species now dealt with are the most important cladocerans of the plankton in lakes in northern Sweden and they have been so abundant in the samples that it has been possible to draw conclusions about their annual cycles. This is not the case of *Polyphemus pediculus, Bythotrephes longimanus,* and *Leptodora Kindtii,* which only occurred in small numbers. What is common to them all is that they are not adult until July or August, when the females are also carrying eggs.

VII. The effect of water-level fluctuations on the zooplankton

A number of investigations have been carried out to ascertain the influence of a regulation on the biological conditions of a lake. It is primarily changes in the fish populations and the bottom fauna that have been treated. The plankton fauna has not been studied to the same extent. Investigations have been made abroad into the conditions of artificial lakes, formed by the damming up of rivers. An extensive work has been published in Czecho-Slovakia (STEPANEK, CHALUPA et al. 1958 and 1959). Although these thorough investigations offer much interesting information, the results are not applicable to the lakes in northern Sweden. The fluctuations of the water level are much more pronounced in the Swedish lakes than in the foreign reservoirs. Results from reservoirs in North America indicate that regulations have only a negligible effect on the plankton fauna (CUERRIER 1954, RAWSON 1958 and others). A small increase in the standing crop was observed after the regulation.

Investigations of regulated lakes of the same kind as the lakes dealt with in this paper have been made in Norway by DAHL (1926, 1933) and HUITFELDT-KAAS (1935). These investigations have, however, been mainly concerned with the influence of regulation on the fish fauna, bottom fauna and the cladocerans of the littoral zone, while the pelagic fauna has not been observed. AASS (1960) on the other hand has taken plankton samples once a year in Limingen (Norway) over a period of five years. He obtained the largest quantities, with one single exception, the year before the regulation (lowering of the water level).

Regulated lakes of northern Sweden have been the object of extensive investigations but quantitative and qualitative data of zooplankton have been lacking until quite recently, when AXELSON (1961 a) published a paper on zooplankton in Ransaren and Kultsjön. He has found that following the regulation of Ransaren there has been a considerable increase in the number of zooplankters as well as in the total volume. According to AXELSON, this increase is due to improvement of the food conditions and also to a reduction of the losses generally caused by the outflow.

The regulation of the lakes in northern Sweden generally involves a filling of the reservoirs in spring and a drawing off of water in winter. There are thus great variations in the water level throughout the year. The amplitude is, for example, in Borgasjön 17 m (see table 3), 16 m above and 1 m below the natural mean water level. Within the littoral zone which is alternatively flooded and dried up, the bottom fauna will change considerably. In Blåsjön, GRIMÅS (1961) has recorded a loss of 70 % of the bottom fauna in this area and of 25 % in the rest of the lake. As char and trout to a great extent feed on bottom organisms, this reduction of the bottom fauna will seriously affect the fish population (RUNNSTRÖM 1955, NILSSON 1961). The char, which even under normal conditions often feeds on plankton, probably adapts itself more easily than trout to the new conditions (NILSSON 1961).

Several authors have stressed the importance for the plankters of the outflow from a lake. RUTTNER (1930) is of opinion that a great deal of plankton, especially the phytoplankton and the rotifers, are swept away by the current of the outflow while bigger plankton animals, the crustaceans, are better able to withstand it. BROOK and WOODWARD (1956), RAWSON (1958) and EINSELE (1960) also state that the standing crop is impoverished by outflow losses.

BROOK and WOODWARD have observed both in field tests and in the laboratory the ability of some crustaceans to avoid the outflow current. Adults proved to resist the current better than young individuals. The cladocerans swim against the current all the time, whereas the copepods start doing so only near the outlet when the force of the current is increasing.

In order to get an idea of the reactions of some species dealt with in this paper a simple experiment has been performed. The species studied are *Cyclops scutifer, Heterocope appendiculata, Daphnia cristata cristata, Bosmina coregoni, Holopedium gibberum.*

For this experiment a tube of plexiglass was used, 1.5 m long with an inner diameter of about 7 cm. At one end it was connected to a water tank. The other end was closed by a rubber stopper through which passed a glass tube. To make it possible to regulate the outflow through the plexiglass tube a rubber tube with a clip was attached to the glass tube. The animals and the water used for the experiments was fetched directly from a lake and the brief transportation can not have impaired the physical condition of the crustaceans. After the plexiglass tube and the tank were filled with water, the reactions of the animals were observed and the rate of the current was regulated by the clip. The rapidity of the current was measured by colour injections into the water (rhodamin). The results of this simple experiment well agree with those obtained by BROOK and WOODWARD. The copepods do not seem to react to running water until just in front of the outlet, where the current accelerated rapidly; here they began to swim vigorously and erratically against the current. The cladocerans, on the other hand, turned as soon as they were placed in the tank and swam against the current. *Daphnia cristata cristata* proved to be able to withstand a current velocity of 18 cm/min. at a temperature of 10.3°C. *Bosmina coregoni* quickly sought refuge at the walls of the tube and then swam against the current. With its gelatinous mantle, *Holopedium gibberum* is the species of cladocerans that is most easily carried away by the current. It is true that objections can be made to the simple arrangements of the experiment but the object has only been to see if the results of BROCK and WOODWARD apply also to the species dealt with in this paper and if the reactions of species in running water show great variations.

No doubt great quantities of plankton are swept out from a lake by the outflow current. However, the water of an impounded lake being stored during summer and autumn, the outflow is less important during this part of the year than before the regulation (Fig. 16). The standing crop of the zooplankton might then be expected to increase in an impounded lake and AXELSON (1961 a, 1963) has proved that that is the case. Observations of the primary production in Ransaren indicate that the regulation brings about an increase (RODHE 1957, 1963), since at the raising and the lowering of the water level, flooding and erosion will add organic matter and inorganic nutrients to the lake.

In the earlier chapter an account has been given of the species composition of the thirteen lakes and an attempt made to establish the annual cycle of some of the most common species. It was then found that there are great differences between the lakes with regard to the composition of the crustacean fauna as well as its development during the summer. It is difficult to draw comparisons between the lakes, as geographical situation, depth etc. differ from lake to lake and, moreover, six of the lakes are regulated. However, an attempt will be made to compare regulated and unregulated lakes as regards the plankton crustaceans.

The size of the standing crop is given as the number of individuals per dm^2 (Fig. 17—18). As the depth varies, it is necessary to compare lakes where samples have been taken down to the same level. The variations noted in the size of the standing crop during summer were mentioned in the chapter on the annual cycle of the species.

Three of the lakes having low quantitative values are Fjosokken, Storuman and Vojmsjön. As all three lakes contain whitefish (Table 2), the possibility cannot be excluded that the somewhat lower quantitative values of the lakes are caused by a grazing effect of the whitefish populations. Vojmsjön e.g. contains three species of whitefish, two of which feed at least partly on plankton (FABRICIUS 1950, SVÄRDSON 1957, NILSSON 1958).

The composition of the plankton community must also be taken into account. In an earlier chapter it was stated that *Daphnia cristata cristata* is numerous in the lakes only in the latter part of the summer, which was assumed to be due to the temperature conditions of the lake. As *D. cristata cristata* is the only representative of the genus present in all the lakes with whitefish, a small population of this cladoceran in these lakes compared to other lakes containing *D. longispina hyalina* may also be due to the temperature factor.

It is of special interest to note that whitefish is the dominating fish species in the lakes containing *Daphnia cristata cristata*. The absence of char may be due to the fact that during the period in spring when the fry is depending on plankton organisms as its food, the resting eggs of *D. cristata cristata*

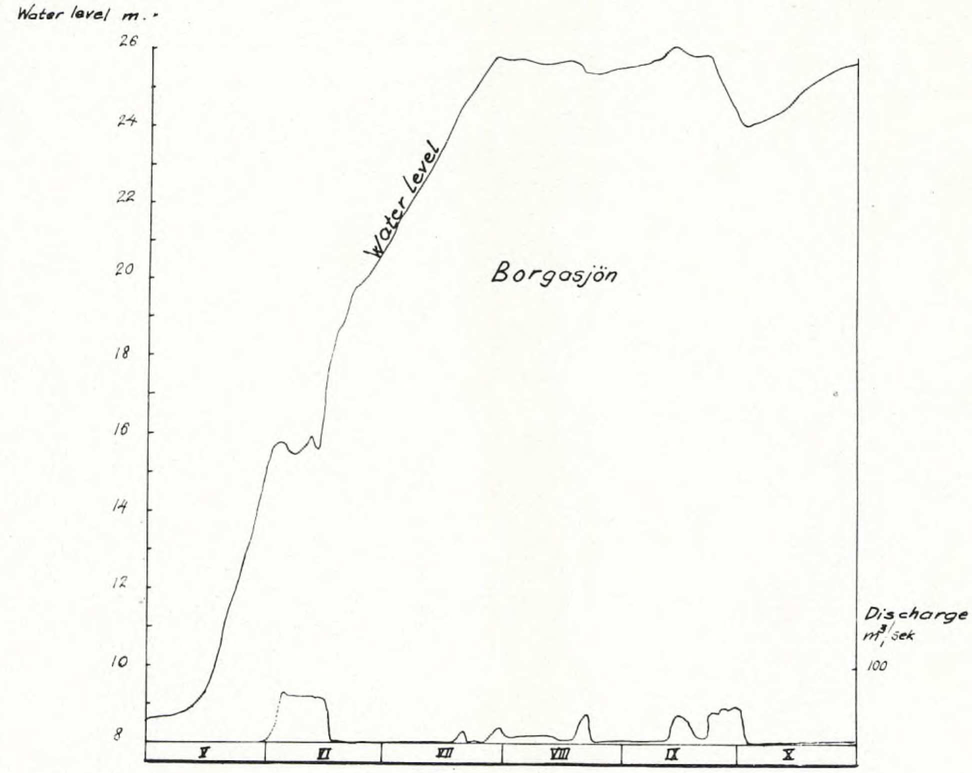


Fig. 16: 1.

Fig. 16: 1—6. Water level and discharge during the period May—October 1957 of the regulated lakes.

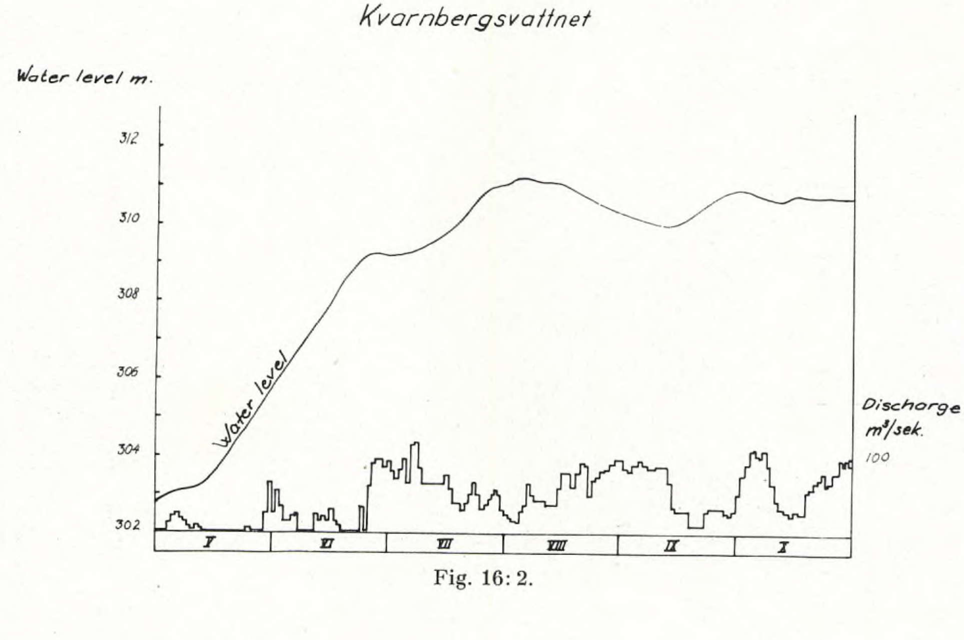


Fig. 16: 2.

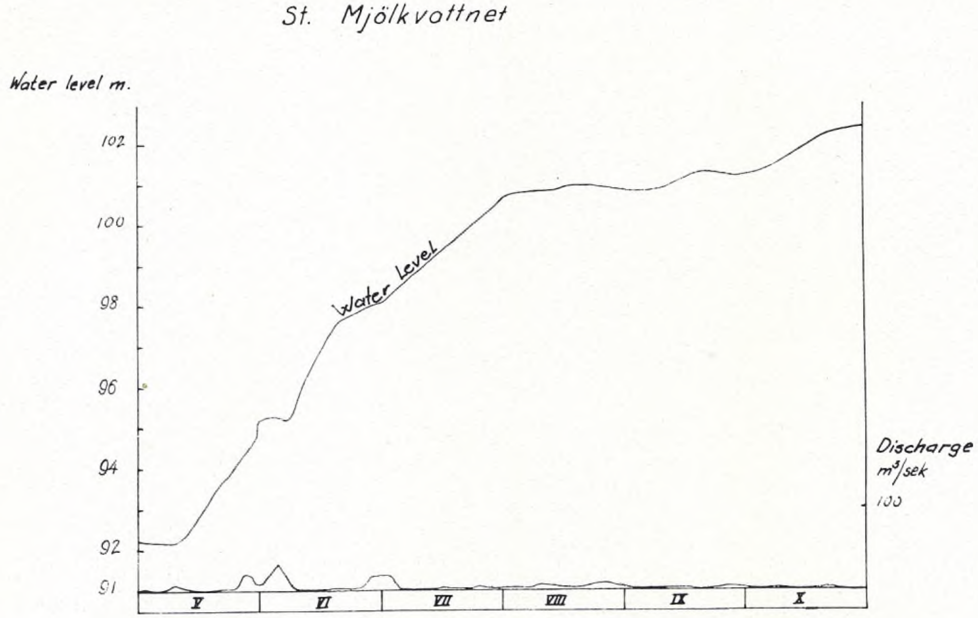


Fig. 16: 3.

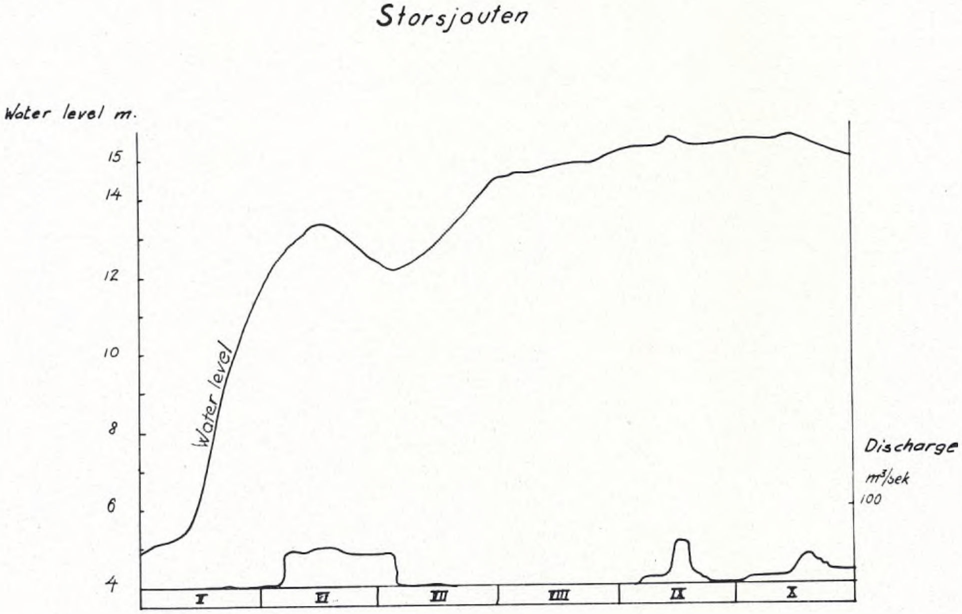


Fig. 16: 4.

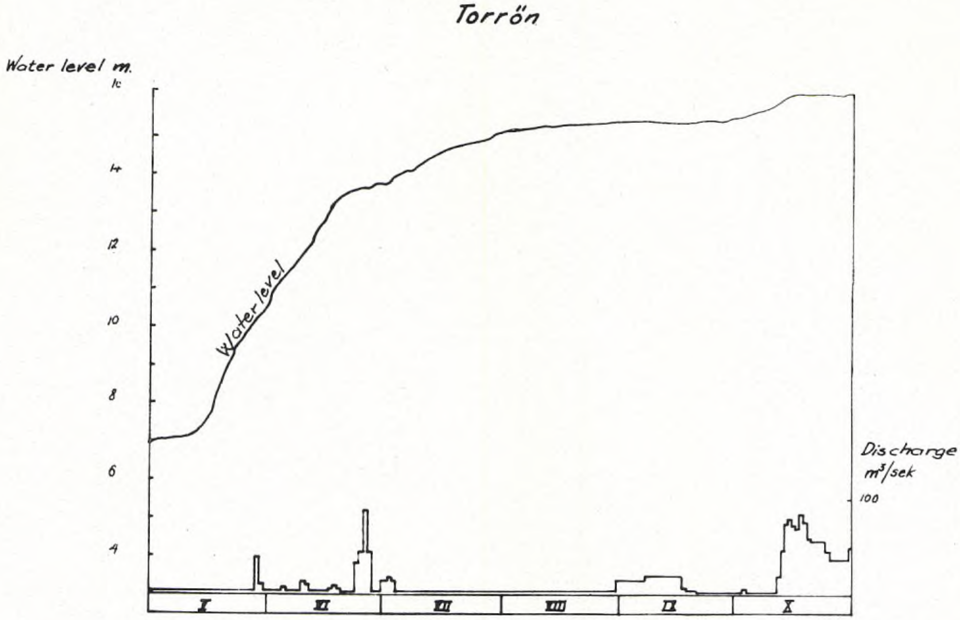


Fig. 16: 5.

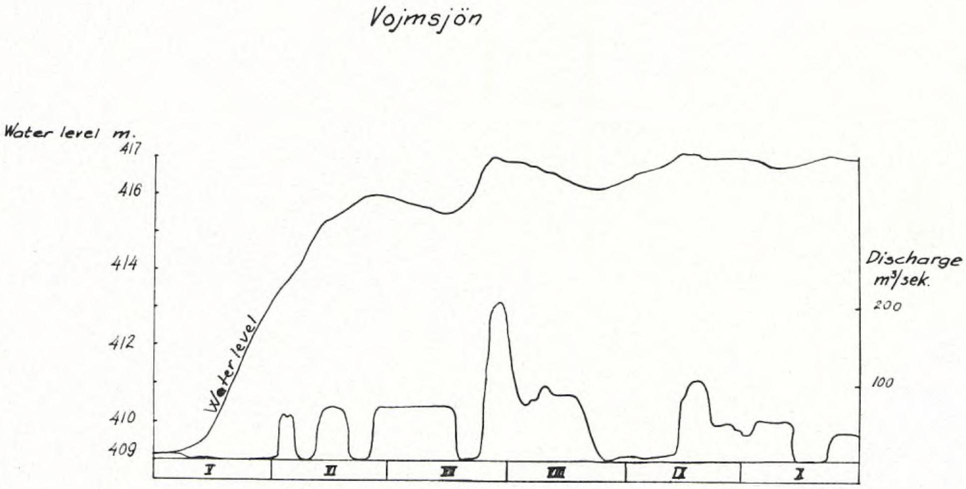


Fig. 16: 6.

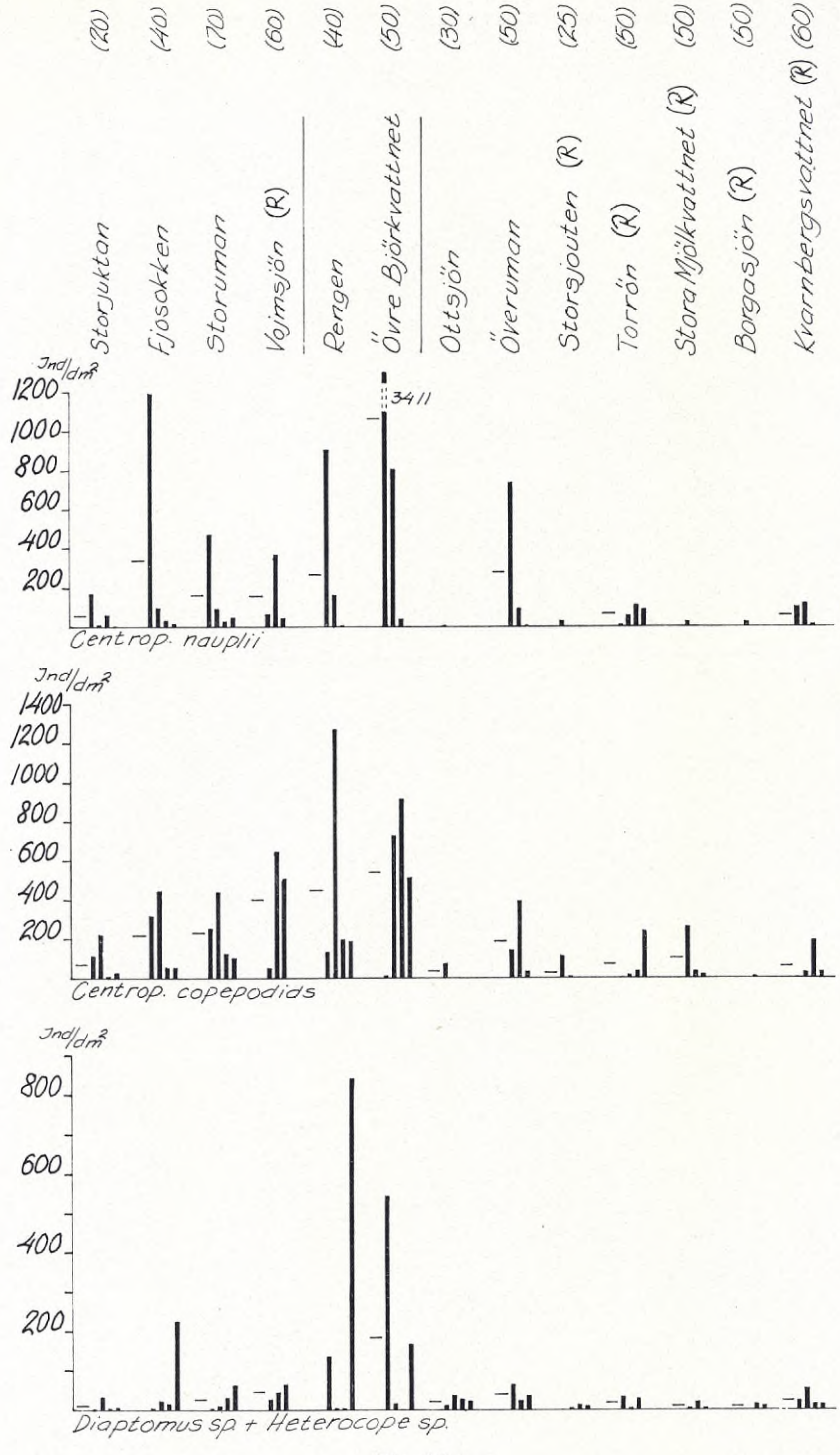


Fig. 17 a.

Fig. 17 a. The abundance of *Diaptomus* sp.+*Heterocope* sp. Lakes with an eurythermal fauna (*Diaptomus graciloides*) are grouped to the left and lakes with a cold stenothermal fauna (*Diaptomus laticeps*) are grouped to the right. The figures within parentheses indicate depth. R=regulated lakes. Rengen and Övre Björkvattnet contain *D. graciloides* as well as *D. laticeps*. Mean numbers are indicated.

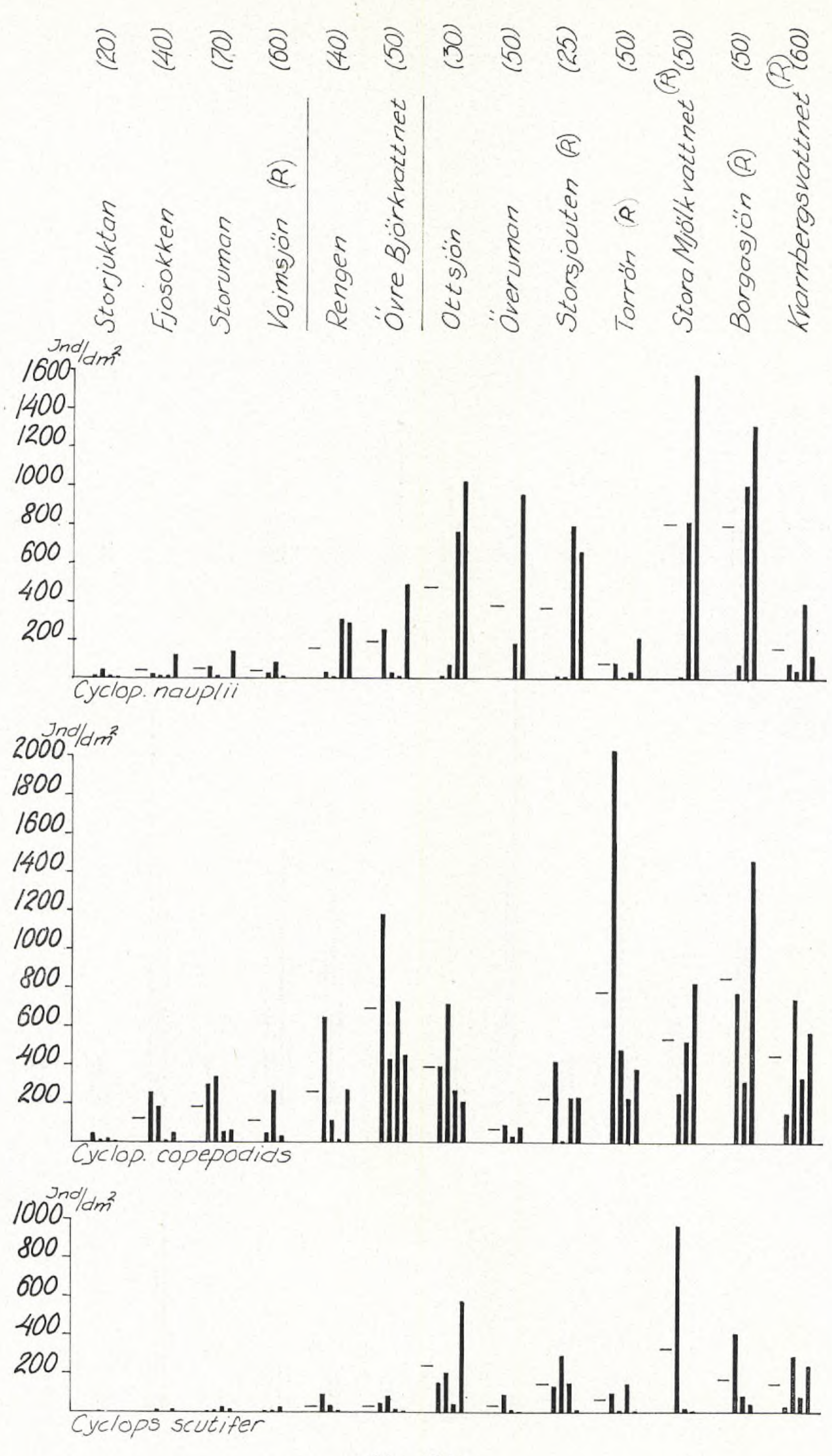


Fig. 17 b.

Fig. 17 b. The abundance of *Cyclops scutifer*. Lakes with an eurythermal fauna are grouped to the left and lakes with a cold stenothermal fauna are grouped to the right. The figures within parentheses indicate depth. R=regulated lakes. Mean numbers are indicated.

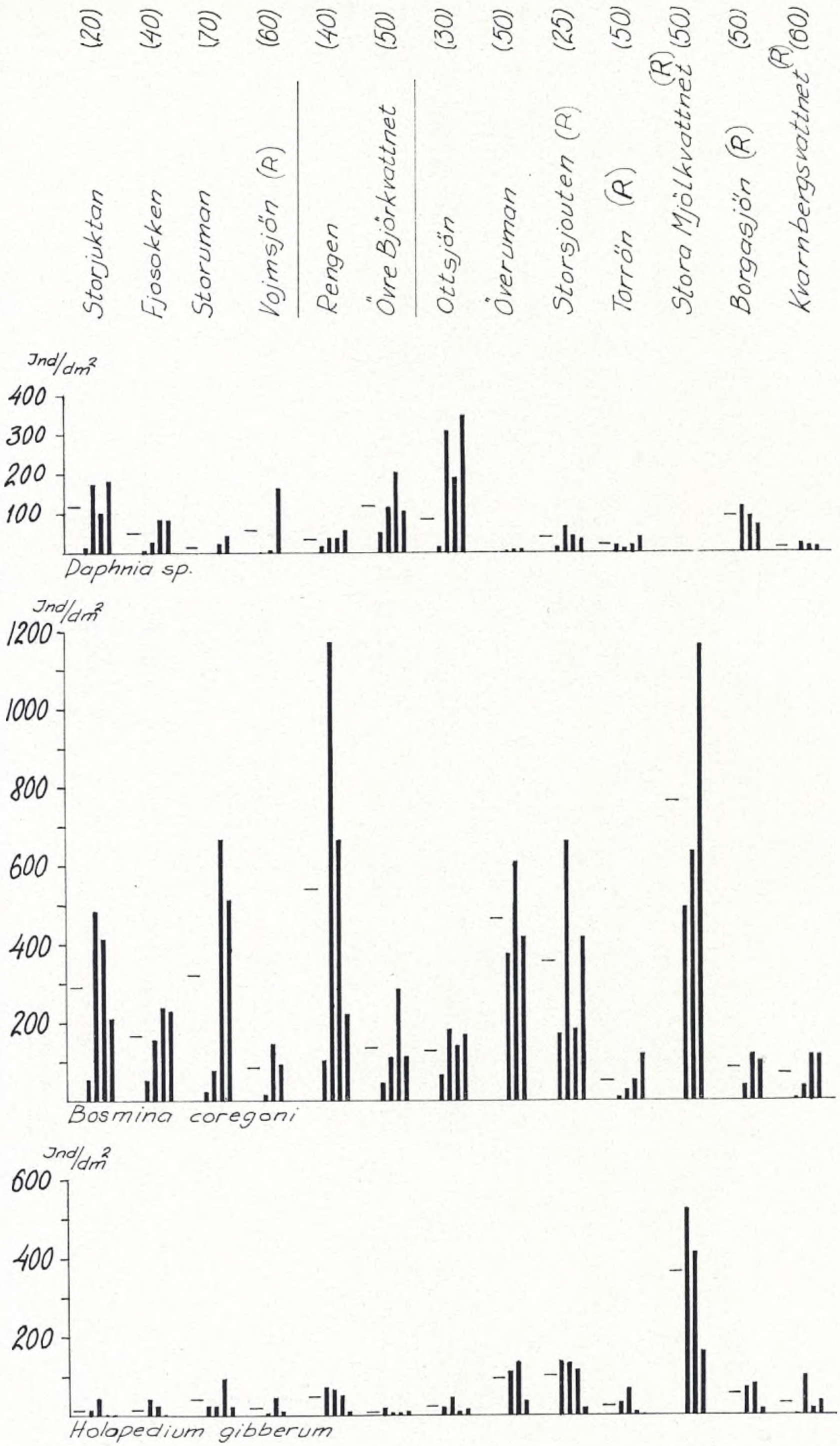


Fig. 18. The abundance of *Daphnia* sp., *Bosmina* coregoni and *Holopedium gibberum*. Lakes with an eurythermal fauna (*Daphnia cristata cristata*) are grouped to the left and lakes with a cold stenothermal fauna (*Daphnia longispina hyalina*) are grouped to the right. The figures within parentheses indicate depth. R=regulated lakes. Mean numbers are indicated.

have not yet been hatched. The hatching of *D. longispina hyalina* probably takes place much earlier.

As to the size of the standing crop of copepods, relatively high values of *Diaptomus* were noted in some lakes while other lakes showed low values. It is again a matter of what species are found in each lake but it must also be borne in mind that the annual cycle of any one species may vary in the different lakes (see previous chapter). The population of a species reproducing in spring will in summer be made up of a great number of nauplii and copepodids. If the reproduction takes place in autumn, there will be a certain natural reduction of the population during winter and spring. Samples from the summer months, containing mainly copepodids, will then not be equally rich in individuals. *Diaptomus graciloides* shows throughout considerably higher quantitative values than *D. laticeps.* As to adult diaptomids only, the somewhat smaller *D. graciloides* has always been more abundant than *D. laticeps,* which is more robust. In chapter IV it was stated that there exist certain differences between the lakes as to the percentual composition of the copepod fauna. In some lakes, the copepods were mainly represented by *Diaptomus*, and in others by *Cyclops* (Fig. 19—31). It can now be established that when *Diaptomus* dominates, it is always as *D. graciloides. Heterocope* never accounts for more than a small part of the copepod community in any of the lakes examined.

As regards the cladocerans, it is further observed that *Holopedium gibberum* is unusually abundant in Stora Mjölkvattnet. The distribution of this species is decided by a great number of factors, some of which are unknown (RYLOV 1935, HAMILTON 1958). Until further knowledge has been acquired about the biology of the species, the importance of the competitive factor must not be left out of account when an explanation of the abundance of *H. gibberum* in Stora Mjölkvattnet is attempted. *Daphnia* is in fact lacking in the lake. For these reasons, *H. gibberum* will not be included in the comparison between regulated and unregulated lakes.

From the evidence given by the thirteen lakes there is nothing to indicate that the crustaceans are more abundant in the zooplankton of a regulated than an unregulated lake. Of the copepods (Fig. 17, table 8), *Diaptomus graciloides* always occurs as already mentioned, in greater numbers than the other *Diaptomus*-species, which explains the maxima of the diagram (Övre Björkvattnet, Fjosokken, Rengen, Storjuktan, Storuman, Vojmsjön). In this diagram *Diaptomus* and *Heterocope* have been grouped together, as the latter is rare. The tendency to a reduced density of plankton in lakes containing whitefish has already been touched upon (compare Fjosokken—Rengen, Storuman—Övre Björkvattnet). That most of the regulated lakes (Borgasjön, Kvarnbergsvattnet, Stora Mjölkvattnet, Storsjouten, Torrön) have small numbers of *Diaptomus* is due to the fact that in these lakes the genus is represented by *D. laticeps* (cf. Ottsjön, unreg. — Storsjouten, reg.). The greatest

Table 8. Mean numbers of individuals/dm² (see fig. 17—18). Figures within parentheses indicating the rank order of the lakes with regard to the mean numbers. R=Regulated lakes.

	Storjuktan	Fjosokken	Storuman	Vojmsjön (R)	Rengen	Övre Björkvattnet	Ottsjön	Överuman	Storsjouten (R)	Torrön (R)	Stora Mjölkvattnet (R)	Borgasjön (R)	Kvarnbergsvattnet (R)
Diaptomus sp.+Heterocope sp. ad.	10 (11)	66 (3)	27 (6)	46 (4)	246 (1)	182 (2)	24 (8)	42 (5)	7 (13)	18 (9)	11 (10)	10 (11)	27 (6)
Cyclops scutifer ad.	<1 (13)	7 (12)	12 (10)	11 (11)	34 (9)	36 (7)	242 (2)	36 (7)	147 (5)	68 (6)	330 (1)	178 (3)	153 (4)
Daphnia sp.	119 (2)	51 (6)	17 (10)	58 (5)	38 (8)	120 (1)	88 (4)	8 (12)	40 (7)	22 (9)	— —	94 (3)	15 (11)
Bosmina coregoni	291 (6)	168 (7)	320 (5)	85 (11)	541 (2)	138 (9)	139 (8)	465 (3)	357 (4)	52 (13)	764 (1)	86 (10)	68 (12)
Holopedium gibberum..	15 (12)	17 (11)	42 (6)	21 (10)	49 (5)	10 (13)	23 (9)	94 (3)	100 (2)	28 (8)	366 (1)	55 (4)	39 (7)

densities of *Cyclops scutifer* seem to be found in lakes containing *Diaptomus laticeps, D. denticornis* or *D. laciniatus* and therefore one may get the impression that there is an increase in *C. scutifer* in regulated lakes. A comparison between Ottsjön and Storsjouten shows on the contrary that *C. scutifer* is more numerous in the unregulated lake. In Borgasjön and Stora Mjölkvattnet high quantitative values have been obtained.

The regulated lakes are no more found to have larger standing crops of cladocerans than the unregulated. The case is rather the contrary. In none of the four lakes where it is found does *Daphnia cristata cristata* occur in great numbers. The reasons have already been discussed and nothing definite can be said as to whether the regulation of Vojmsjön has affected the population of *D. cristata cristata.* On the other hand it must be supposed that the regulation has had some influence on *D. longispina hyalina*, in Storsjouten, Torrön, and Kvarnbergsvattnet, lakes where very low quantitative values have been noted (Fig. 18, table 8). Ottsjön could be compared to Storsjouten as their zooplankton contains the same species. Whether or not the total lack of *Daphnia* in Stora Mjölkvattnet is accounted for by the impoundment of the lake cannot be stated with any certainty. LUNDQVIST (1936) characterizes the plankton in this lake as *Holopedium-Polyphemus* plankton and has not found any specimen of the genus *Daphnia. Bosmina coregoni* seems also to be more rare in regulated lakes (Borgasjön, Kvarnbergsvattnet, Torrön, Vojmsjön). Stora Mjölkvattnet and Storsjouten are, however, exceptions in this respect. As regards Stora Mjölkvattnet, this may be explained by the lack of *Daphnia,* its competitor for food, and as for Storsjouten, the depth conditions of this shallow lake may favour *B. coregoni.* No other explanation of the prominent position of *B. coregoni* in these lakes can at present be advanced.

Thus no results have come of the investigation to indicate that the standing crop of zooplankton is larger in regulated lakes than in comparable unregulated lakes. In regard to the copepods there are no great differences between regulated and unregulated lakes. On the other hand, the regulation seems to have a reducing effect on the populations of *Daphnia longispina hyalina* and *Bosmina coregoni* in many lakes.

These results are quite contradictory to those achieved by AXELSON (1961 a) in Ransaren. It is necessary to point out that AXELSON made his investigation just before and just after the regulation of Ransaren. The regulated lakes of the present investigation have been regulated for a number of years (see table 1) which will probably satisfactorily explain the differences in the results. The increase in the standing crop of zooplankton found in Ransaren during the years immediately following the regulation, is, according to AXELSON, due to reduced losses through outflow during the summer as well as to improved food conditions. As mentioned earlier, the damming up of Ransaren caused an increase in the primary production by addition of new organic and inorganic matter from the flooded area. The observations of the primary production have not been carried on long enough to be able to find out how long these favourable conditions for primary production prevail. It may, however, be supposed that the addition of nutrients from the flooded area will gradually cease as the zone is exhausted. The zooplankton will then probably show the same values as before regulation. Even if losses are small in summer, owing to negligible drawing off of water, the food factor will limit the increase of the populations. No definite explanation can be given of the fact that *Daphnia longispina hyalina* and *Bosmina coregoni* are not so numerous in some of the regulated as in comparable unregulated lakes. During the latter part of the autumn, when the drawing off starts, the copepods have either laid their resting eggs, which gather on the bottom, or else the copepods hibernate as copepodids and probably stay in the layers close to the bottom (ELGMORK 1955, 1959). On the other hand, there will still be ephippium-carrying females of *Daphnia* in the upper water layers and it is possible that they will be more affected by the outflow after the regulation. This applies to an even greater extent to the liberated ephippia, which are carried towards the outlet by the wind and the current, a tendency that will be still more pronounced since ice formation takes place later after a regulation. Moreover, ephippia carried onto the shore, may be drained when the water level is lowered during winter. Ephippia can indeed stand draining as well as freezing but the fact must not be overlooked that a considerable lowering of the water level may imply the loss of ephippia. Also in the case of *Bosmina coregoni* the drawing off of water in the autumn may have a reducing effect on the population. As *B. coregoni* does not only belong to the purely pelagical fauna but is also characteristic of the littoral zone (LINDSTRÖM 1957, AXELSON 1961 a) the possibility cannot be excluded that the changes occasioned by the regulation in this zone can have a negative influence on the population. The regulation may even have an indirect effect on the cladocerans. Through the elimination of many bottom organisms which are of great importance as fish food, the char will feed on cladocerans, especially in late summer and autumn (NILSSON 1961). It is impossible to state whether this grazing is of such an extent as to have a noticeable effect on the populations.

Another factor which may be of biological importance is the turbidity of the water that occurs in connection with the construction of a dam and the erosion of the flooded areas. The increased turbidity of the water may be supposed to have a damaging effect on filter feeding crustaceans as the filtering apparatus may be clogged. The effects of a regulation on bottom living filter feeders have been discussed by GRIMÅS (1961).

The changes in the plankton fauna occasioned by the regulation of a lake may be attributed to various factors. It is impossible so far to state which factor is most important. There are probably several operating at the same time with varying effects in different lakes. Future investigations will show what these factors are.

Acknowledgements

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Summary

1. Plankton samples taken by means of a Clarke-Bumpus sampler during the months June—September in thirteen North-Swedish lakes have been analysed with regard to the crustaceans. The material consists in all of some 450 samples distributed on 48 vertical series.

2. Eleven species of copepods and eleven species or subspecies of cladocerans have been found. Chydorids, of which there were very few in the samples, have not been taken into account.
3. The lakes may be divided into two groups as regards the species composition of the fauna. One group includes the cold stenothermal species *Diaptomus laticeps, Heterocope saliens* or *H. borealis* (in one lake) and *Daphnia longispina hyalina* and the other *Diaptomus graciloides, Heterocope appendiculata* and *Daphnia cristata cristata*. Species common for all the lakes are *Cyclops scutifer, Bosmina coregoni* and *Holopedium gibberum* (Table 3—4).
4. The zooplankton community is made up of a small number of crustacean species. During June—September the mean number for *Copepoda* is 3.2 species and for *Cladocera* 4.8 species.
5. In six lakes there have been found two and in one lake three *Diaptomus* species. *Diaptomus graciloides* and *D. laticeps* were the species most often found together, which is probably due to the spreading of *D. laticeps* from lakes situated further up in the same water system.
6. There is a marked relation of dominance within the plankton community. The species that on any one occasion is found to be dominating within the *Copepoda* or *Cladocera* group seldom represents less than 50 % of all the copepods or cladocerans respectively (Table 7, Fig. 19—31).
7. In the lakes where *Diaptomus* dominates over *Cyclops,* it was always found to be *D. graciloides*.
8. A special investigation of the diurnal migration of some crustaceans has given results that confirm CUSHING's theory of midnight sinking and dawn rise (Fig. 6—7).
9. *Diaptomus graciloides* has two generations in one lake (fig. 9) but is monocyclic in the other lakes. In the latter lakes the species has its reproduction period in spring and early summer and probably hibernates as adult but not sexually mature individuals (Fig. 8).
10. The annual cycle of *Diaptomus laticeps* shows certain variations. In some lakes it has its reproduction period in spring, in others in autumn. Results indicate that the population of one lake may be divided into two fractions having different annual cycles.
11. In five of the lakes the population of *Cyclops scutifer* is divided into two fractions, one having its reproduction period in spring, the other in autumn (Fig. 10). In the remaining lakes this dualism is not clearly marked. In these lakes one fraction is not very prominent and in some cases it may be questioned whether there is a dualism in the *Cyclops* population (Fig. 11).
12. The parthenogenetical development of *Daphnia cristata cristata* seems to begin only at a water temperature of about 8°C, which may be the reason

for which this cladoceran shows very low quantitative values in the North-Swedish lakes during summer.

13. From the evidence given by the thirteen lakes there is nothing to indicate that the crustaceans are more abundant in the zooplankton of a regulated than an unregulated lake. As regards the copepods there is no marked difference (Fig. 17 a and 17 b, table 8). In most regulated lakes *Daphnia longispina hyalina* as well as *Bosmina coregoni* show low quantitative values. It has not been possible to state the reason for this reduction of the cladocerans, but some possible factors have been discussed (Fig. 18 and table 8).

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Fig. 19—31. Percentage composition of the zooplankton community (Crustacea).

Appendix: Fig. 32—44. Vertical distribution of the different species (and stages) at midnight in the thirteen lakes (individuals/m^2). In fig. 36 the dashed lines mean that sampler's not functioning on the sampling occasion.

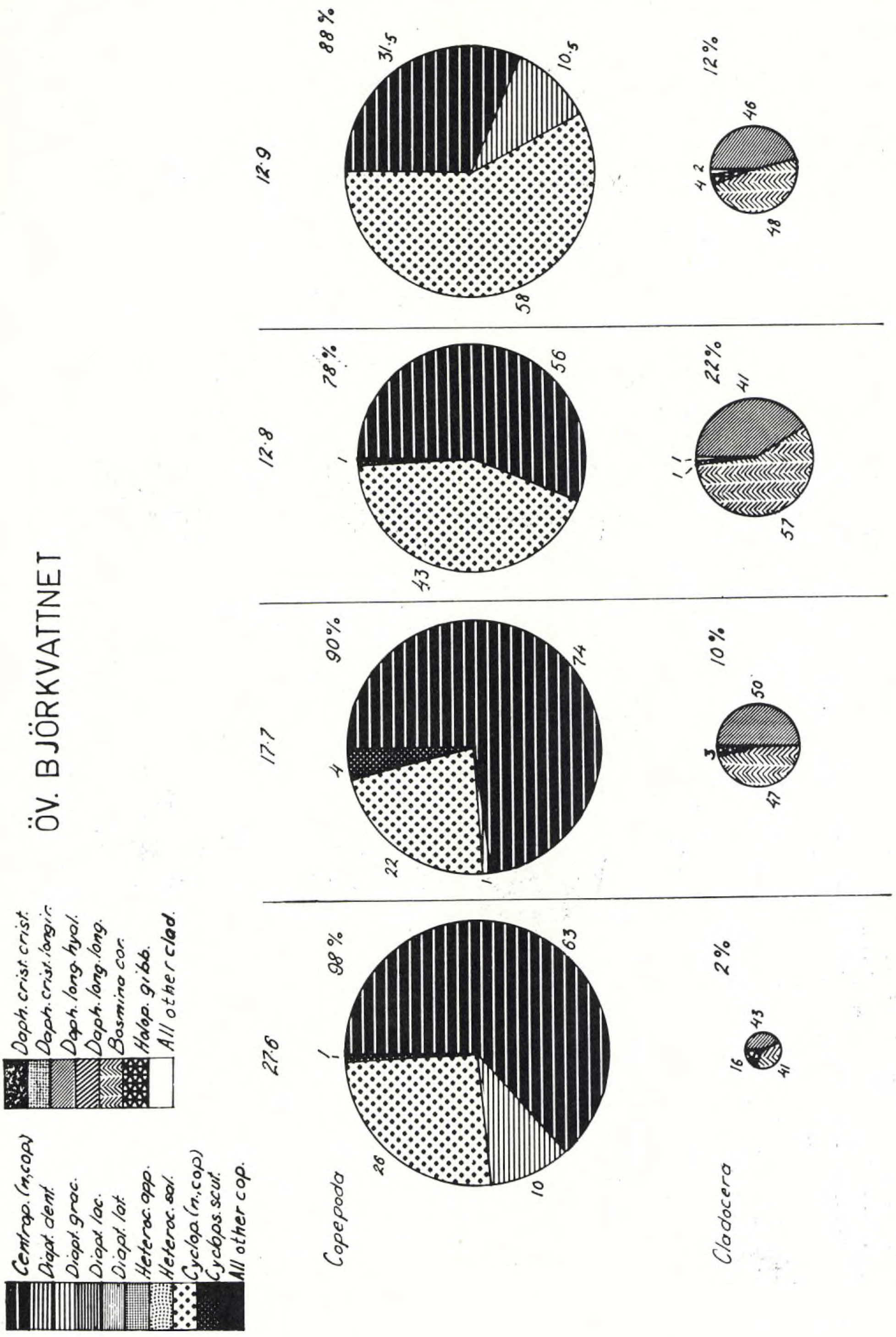

ÖV. BJÖRKVATTNET
Centrop. (n.,cop.)
Diapt. dent.
Diapt. grac.
Diapt. lac.
Diapt. lat.
Heteroc. app.
Heteroc. sal.
Cyclop. (n.,cop.)
Cyclops. scut.
All other cop.
Daph. crist. crist.
Daph. crist. longir.
Daph. long. hyal.
Daph. long. long.
Bosmina cor.
Holop. gibb.
All other clad.
Copepoda
Cladocera
27.6
98 %
1
63
26
10
2 %
16
43
41
17.7
90 %
4
74
22
1
10 %
50
3
47
12.8
78 %
1
56
43
22 %
41
1
1
57
12.9
88 %
31.5
10.5
58
12 %
46
4
2
48

Fig. 19.

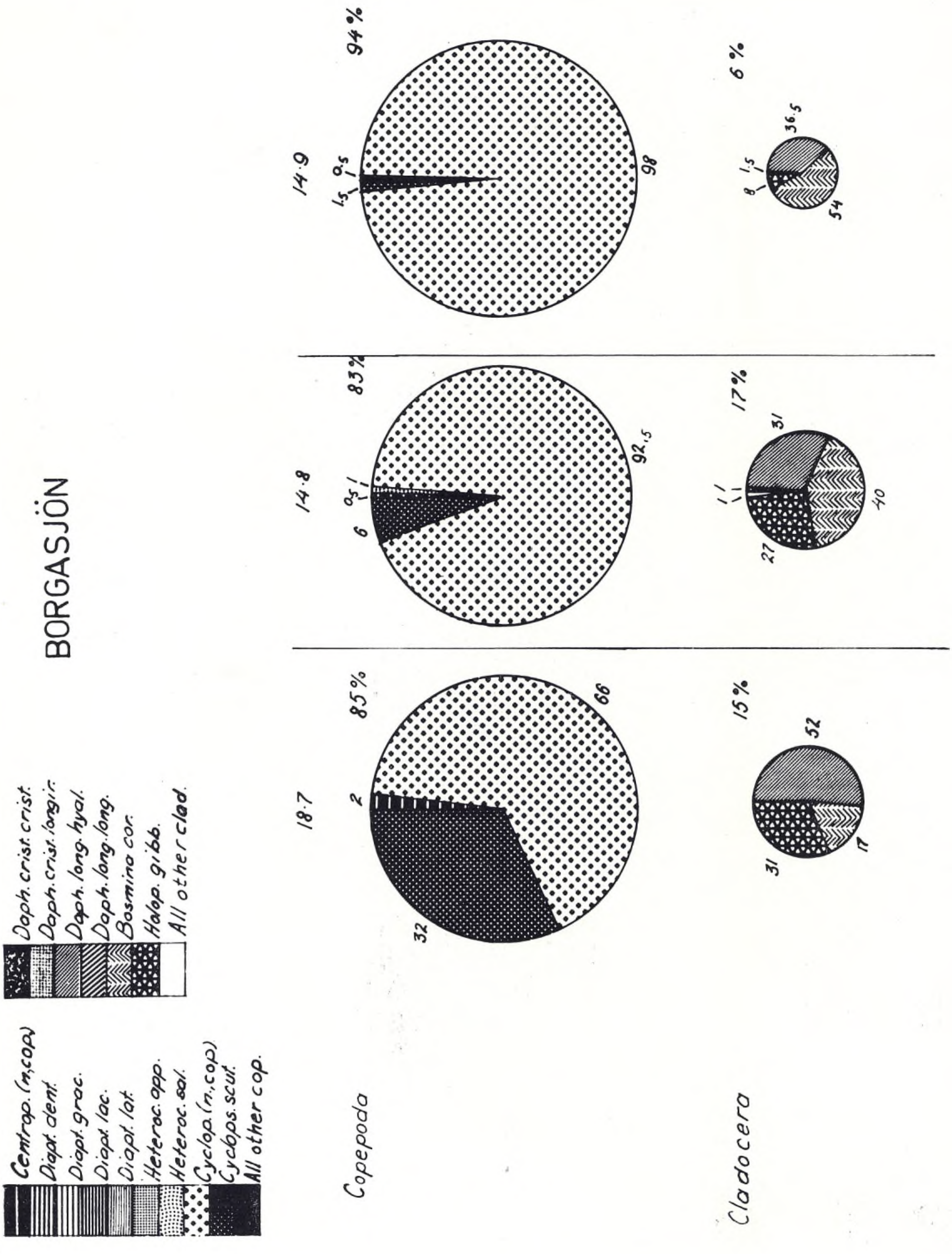

BORGASJÖN
Centrop. (n,cop)
Diapt. dent.
Diapt. grac.
Diapt. lac.
Diapt. lat.
Heteroc. app.
Heteroc. sal.
Cyclop. (n,cop)
Cyclops. scut.
All other cop.
Daph. crist. crist.
Daph. crist. longir.
Daph. long. hyal.
Daph. long. long.
Bosmina cor.
Halop. gibb.
All other clad.
Copepoda
Cladocera
18.7
85%
2
32
66
15%
52
31
17
14.8
83%
0.5
1
6
92.5
17%
31
1
1
27
40
14.9
94%
0.5
1.5
98
6%
36.5
1.5
8
54

Fig. 20.

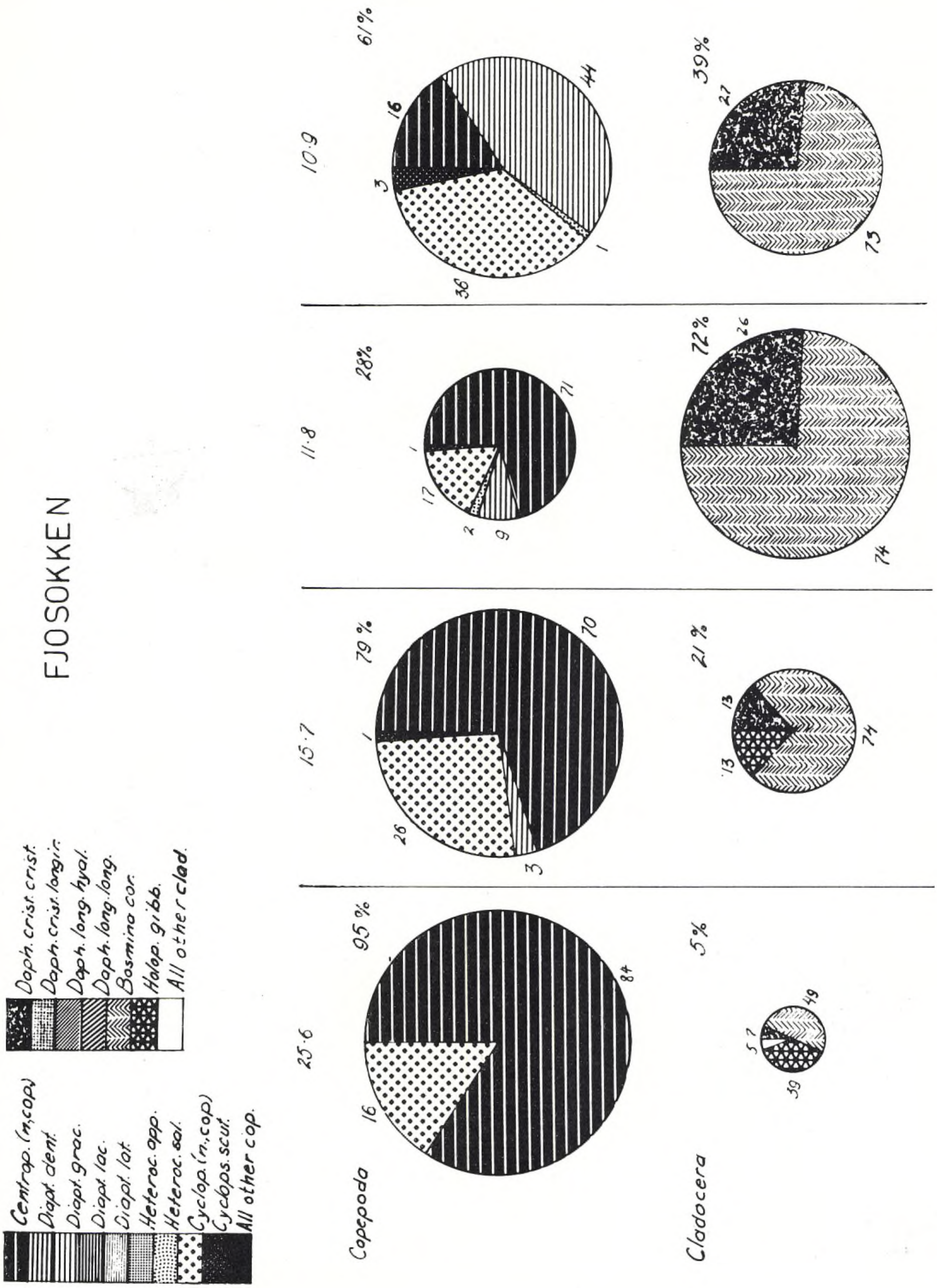
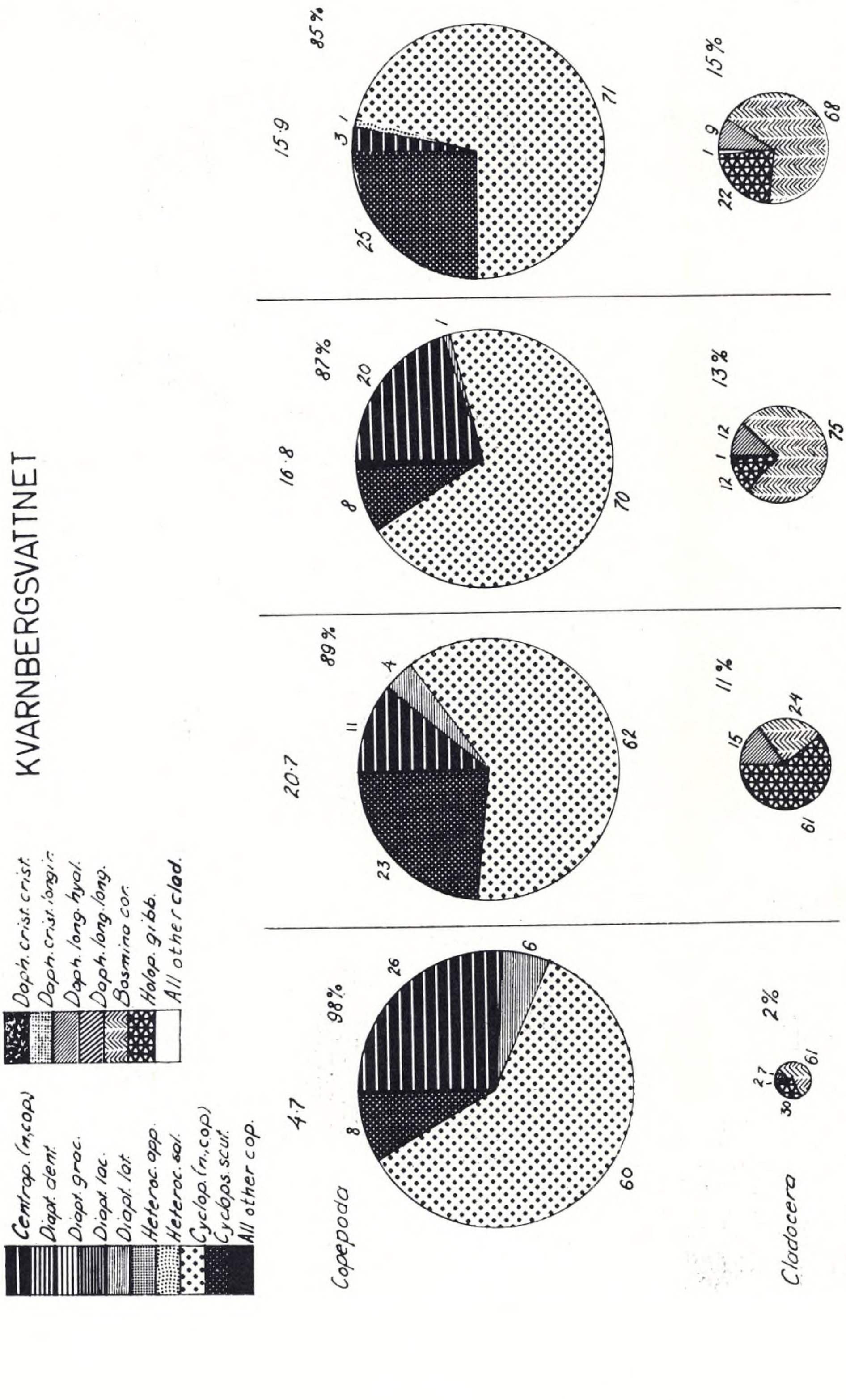

FJOSOKKEN
Centrop. (n,cop.)
Diapt. dent.
Diapt. grac.
Diapt. lac.
Diapt. lat.
Heteroc. opp.
Heteroc. sal.
Cyclop. (n,cop.)
Cyclops. scut.
All other cop.
Daph. crist. crist.
Daph. crist. longir.
Daph. long. hyal.
Daph. long. long.
Bosmina cor.
Holop. gibb.
All other clad.
Copepoda
Cladocera
25·6
95%
16
84
5%
39
5
7
49
15·7
79%
1
26
3
70
21%
13
13
74
11·8
28%
1
17
2
9
71
72%
26
74
10·9
61%
16
3
36
1
44
39%
27
73

Fig. 21.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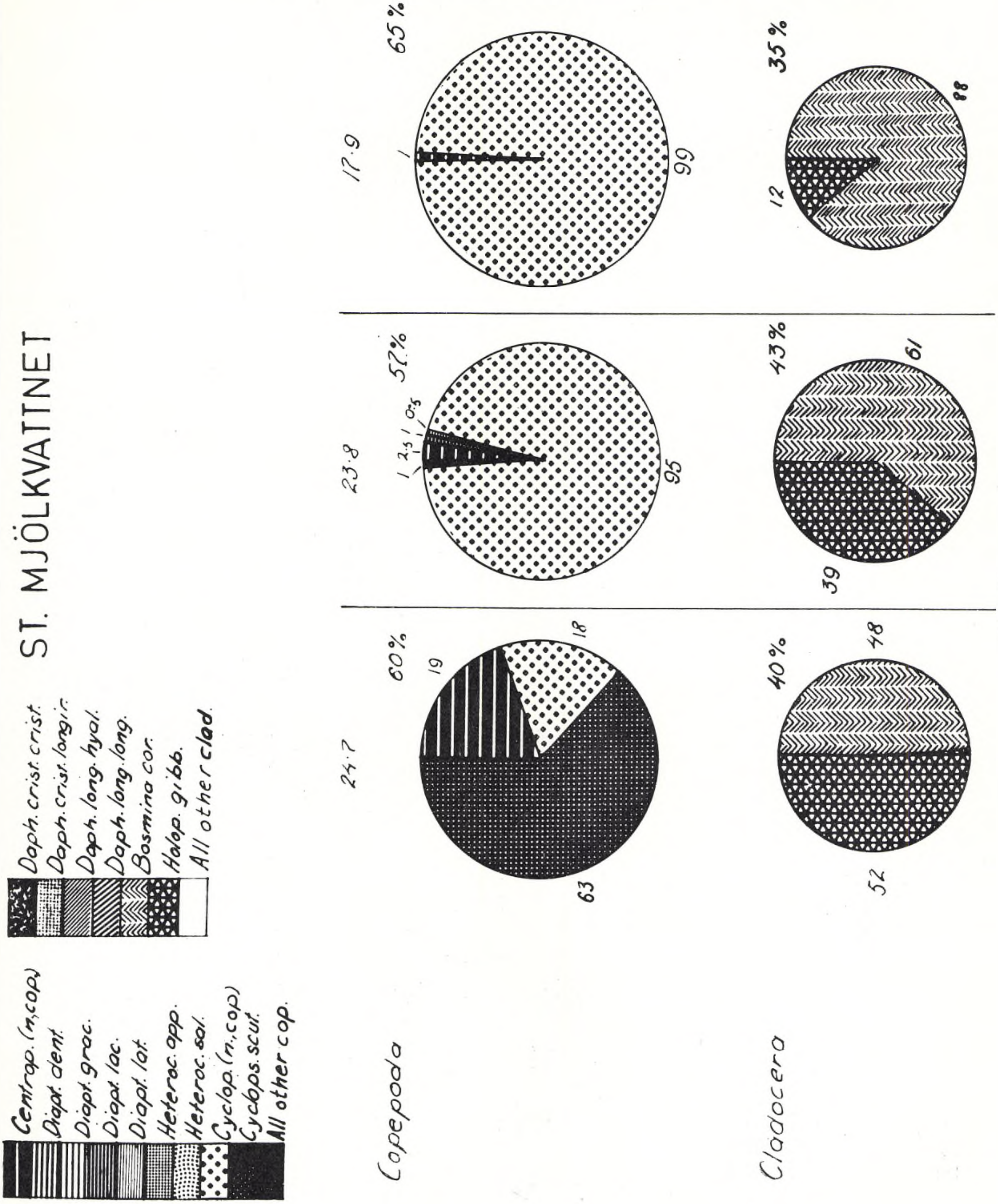
Heteroc. sal.
Cyclop. (n, cop.)
Cyclops. scut.
All other cop.
Daph. crist. crist.
Daph. crist. longir.
Daph. long. hyal.
Daph. long. long.
Bosmina cor.
Holop. gibb.
All other clad.
Copepoda
Cladocera
4·7
98%
8
26
6
60
2%
2
7
30
61
20·7
89%
23
11
4
62
11%
15
24
61
16·8
87%
8
20
1
70
13%
12
1
12
75
15·9
85%
25
3
1
71
15%
22
1
9
68

Fig. 22.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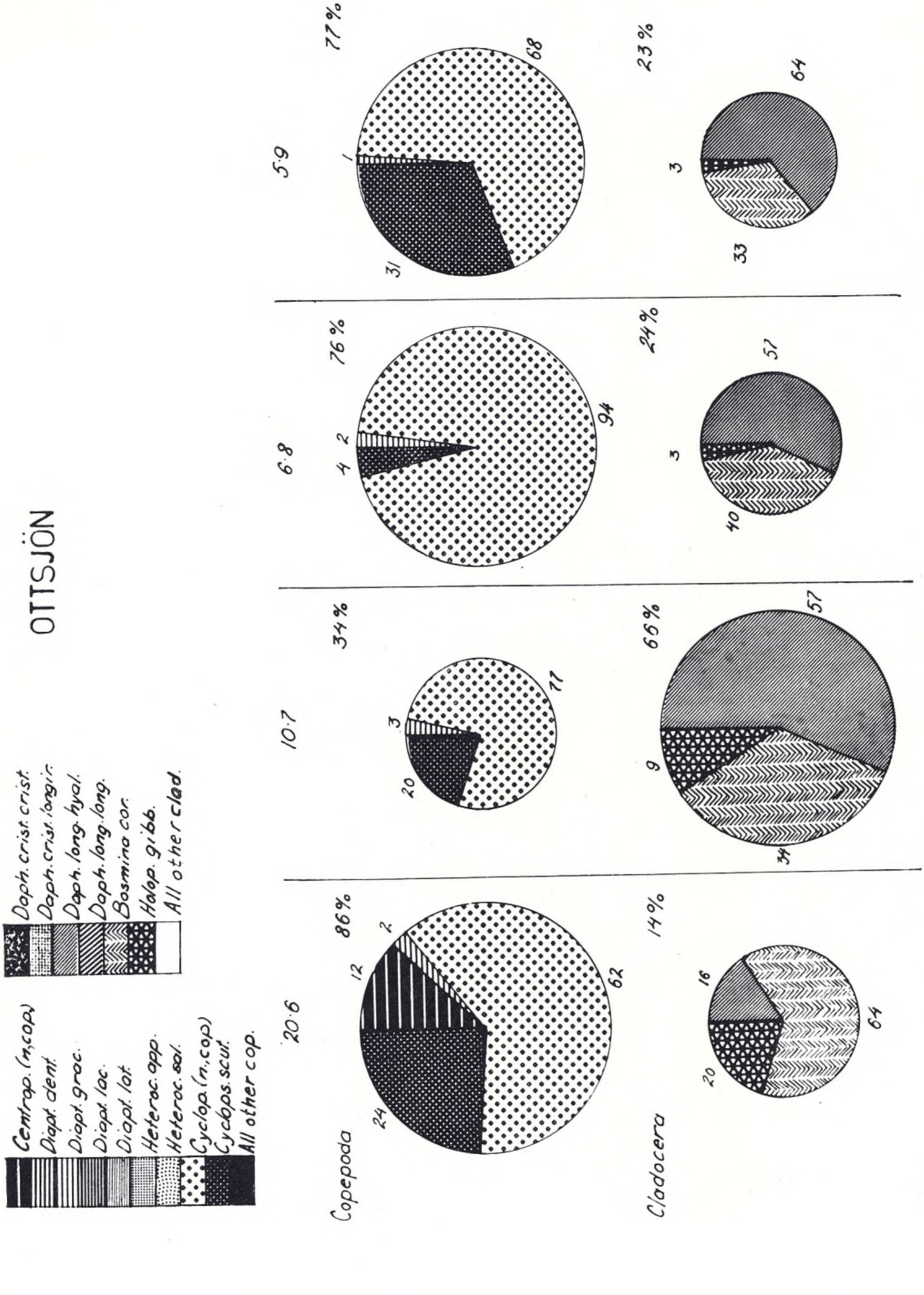
Diapt. lat.
Heteroc. app.
Heteroc. sal.
Cyclop. (n., cop.)
Cyclops. scut.
All other cop.
Daph. crist. crist.
Daph. crist. longir.
Daph. long. hyal.
Daph. long. long.
Bosmina cor.
Holop. gibb.
All other clad.
Copepoda
Cladocera
24.7
60%
19
18
63
40%
48
52
23.8
57%
1
2.5
1
0.5
95
43%
61
39
17.9
65%
1
99
35%
88
12

Fig. 23.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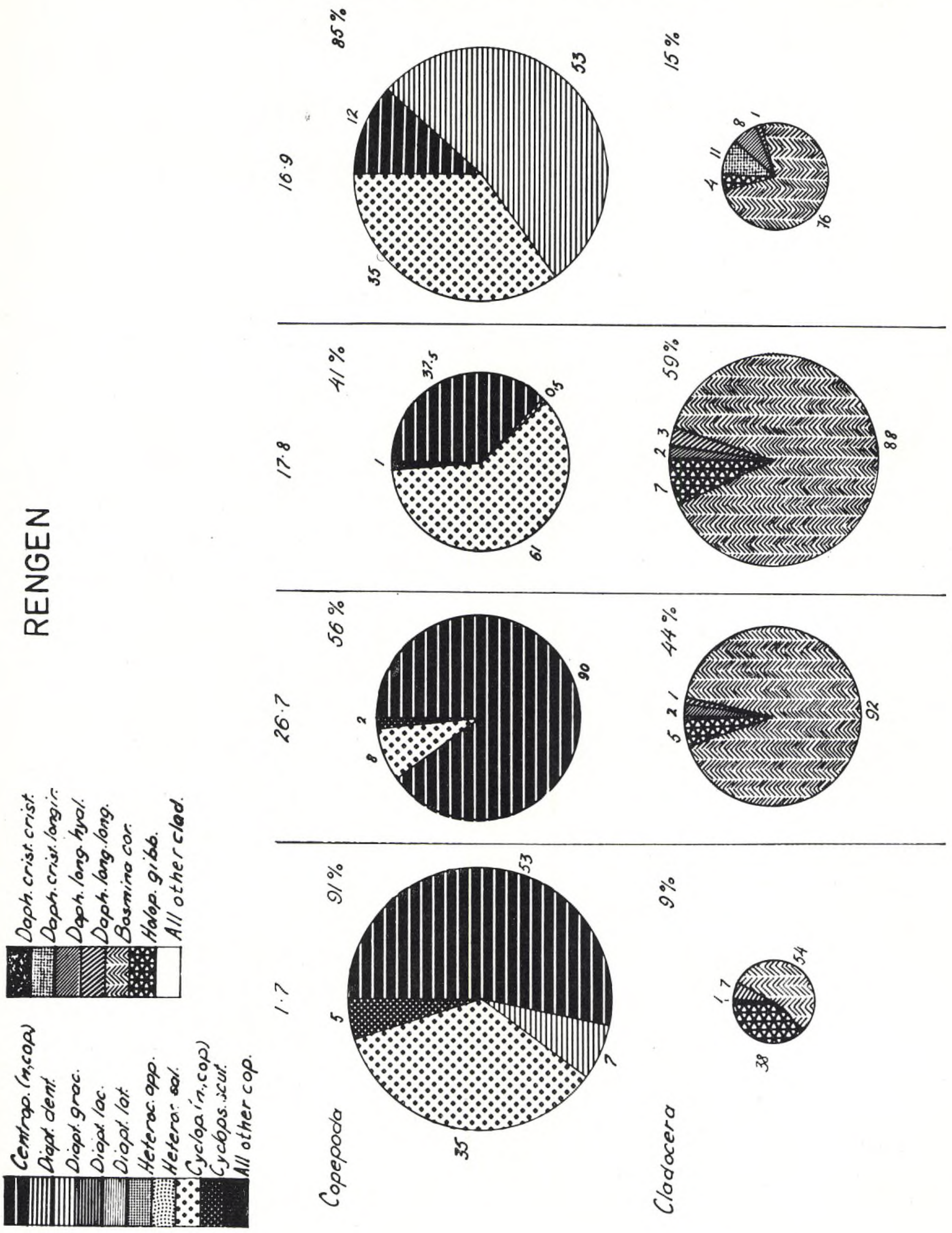
Diapt. lat.
Heteroc. app.
Heteroc. sal.
Cyclop. (n,cop)
Cyclops. scut.
All other cop.
Daph. crist. crist.
Daph. crist. longir.
Daph. long. hyal.
Daph. long. long.
Bosmina cor.
Holop. gibb.
All other clad.
Copepoda
Cladocera
20·6
86%
24
12
2
62
14%
16
20
64
10·7
34%
20
3
77
66%
9
34
57
6·8
76%
4
2
94
24%
3
40
57
5·9
77%
1
31
68
23%
3
33
64

Fig. 24.


RENGEN
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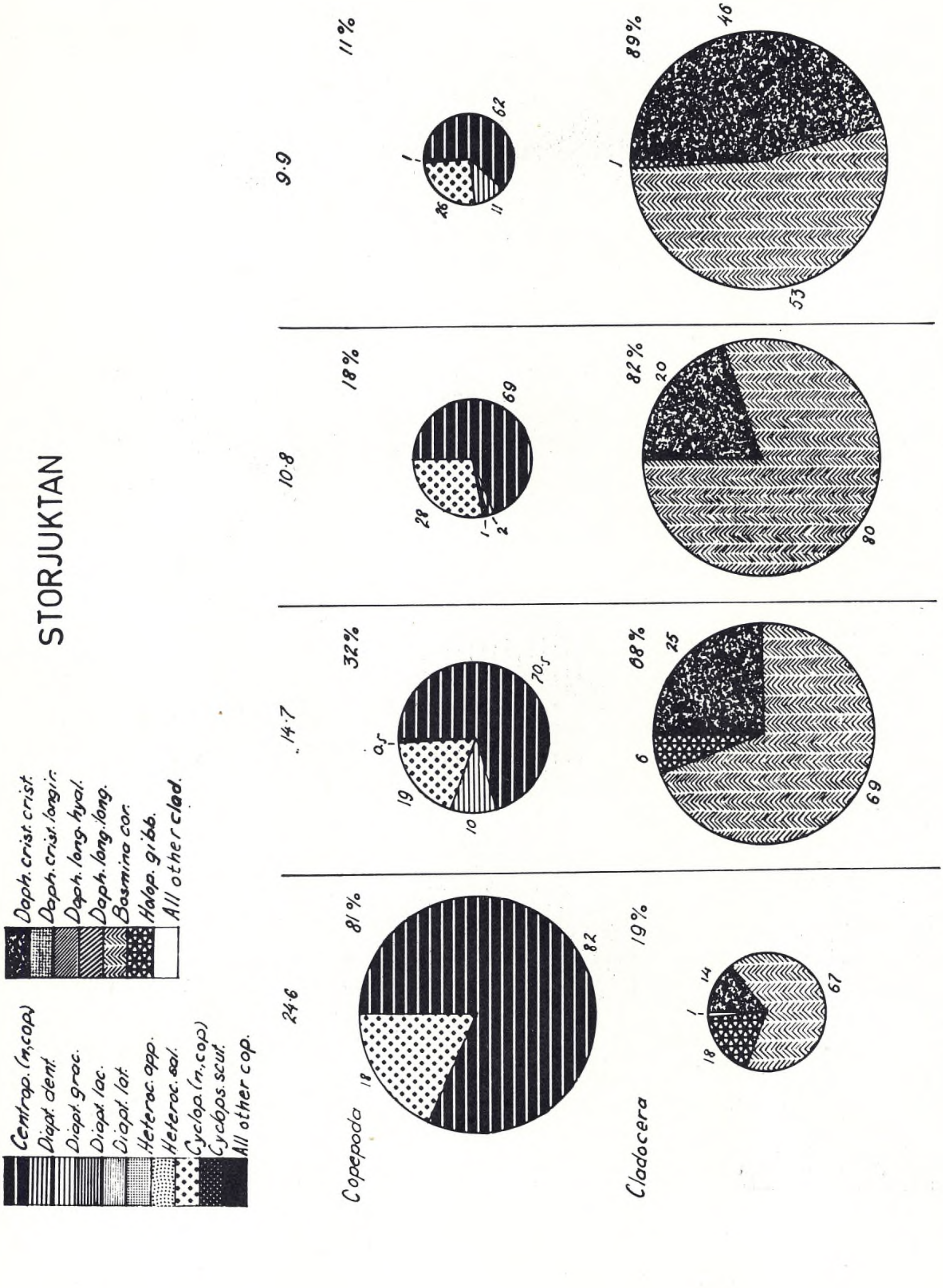
Diapt. lat.
Heteroc. app.
Heteroc. sal.
Cyclop. (n,cop.)
Cyclops. scut.
All other cop.
Daph. crist. crist.
Daph. crist. longir.
Daph. long. hyal.
Daph. long. long.
Bosmina cor.
Holop. gibb.
All other clad.
Copepoda
Cladocera
1.7
91%
53
5
35
7
9%
1
7
38
54
26.7
56%
2
8
90
44%
5
2
1
92
17.8
41%
37.5
0.5
1
61
59%
7
2
3
88
16.9
85%
12
53
35
15%
8
1
11
4
76

Fig. 25.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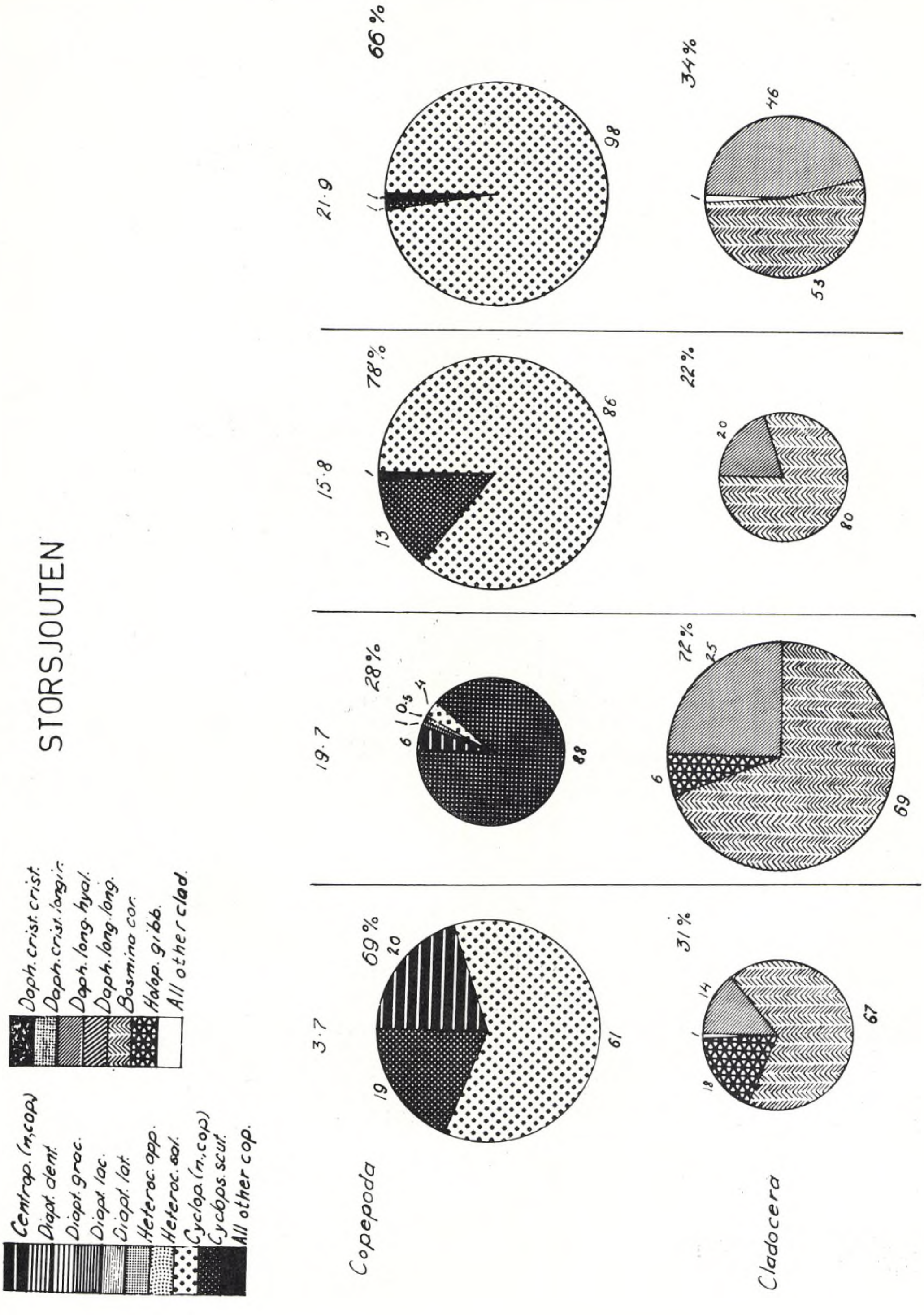
Heteroc. sal.
Cyclop. (n,cop)
Cyclops. scut.
All other cop.
Daph. crist. crist.
Daph. crist. longir.
Daph. long. hyal.
Daph. long. long.
Bosmina cor.
Holop. gibb.
All other clad.
Copepoda
Cladocera
24·6
81%
18
82
19%
18
1
14
67
14·7
32%
0.5
19
10
70.5
68%
6
25
69
10·8
18%
28
1
2
69
82%
20
80
9·9
11%
46
1
11
62
89%
46
1
53

Fig. 26.


STORSJOUTEN
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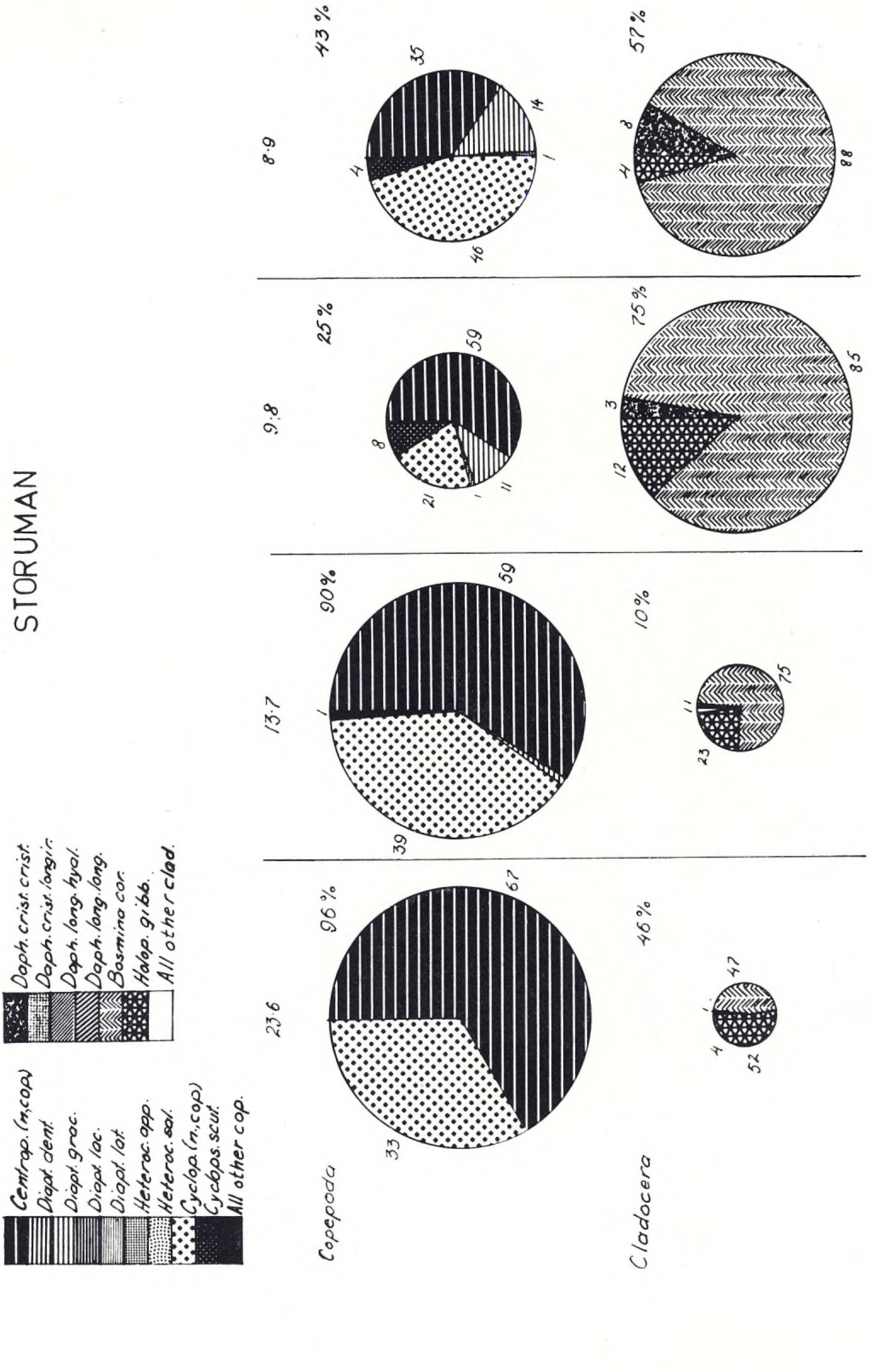
Diapt. grac.
Diapt. lac.
Diapt. lat.
Heteroc. app.
Heteroc. sal.
Cyclop. (n.,cop.)
Cyclops. scut.
All other cop.
Daph. crist. crist.
Daph. crist. longir.
Daph. long. hyal.
Daph. long. long.
Bosmina cor.
Holop. gibb.
All other clad.
Copepoda
Cladocera
3.7
69 %
19
20
61
31 %
1
14
18
67
19.7
28%
6
1
0.5
4
88
72 %
25
6
69
15.8
78%
1
13
86
22%
20
80
21.9
66 %
1
1
98
34%
46
1
53

Fig. 27.


STORUMAN
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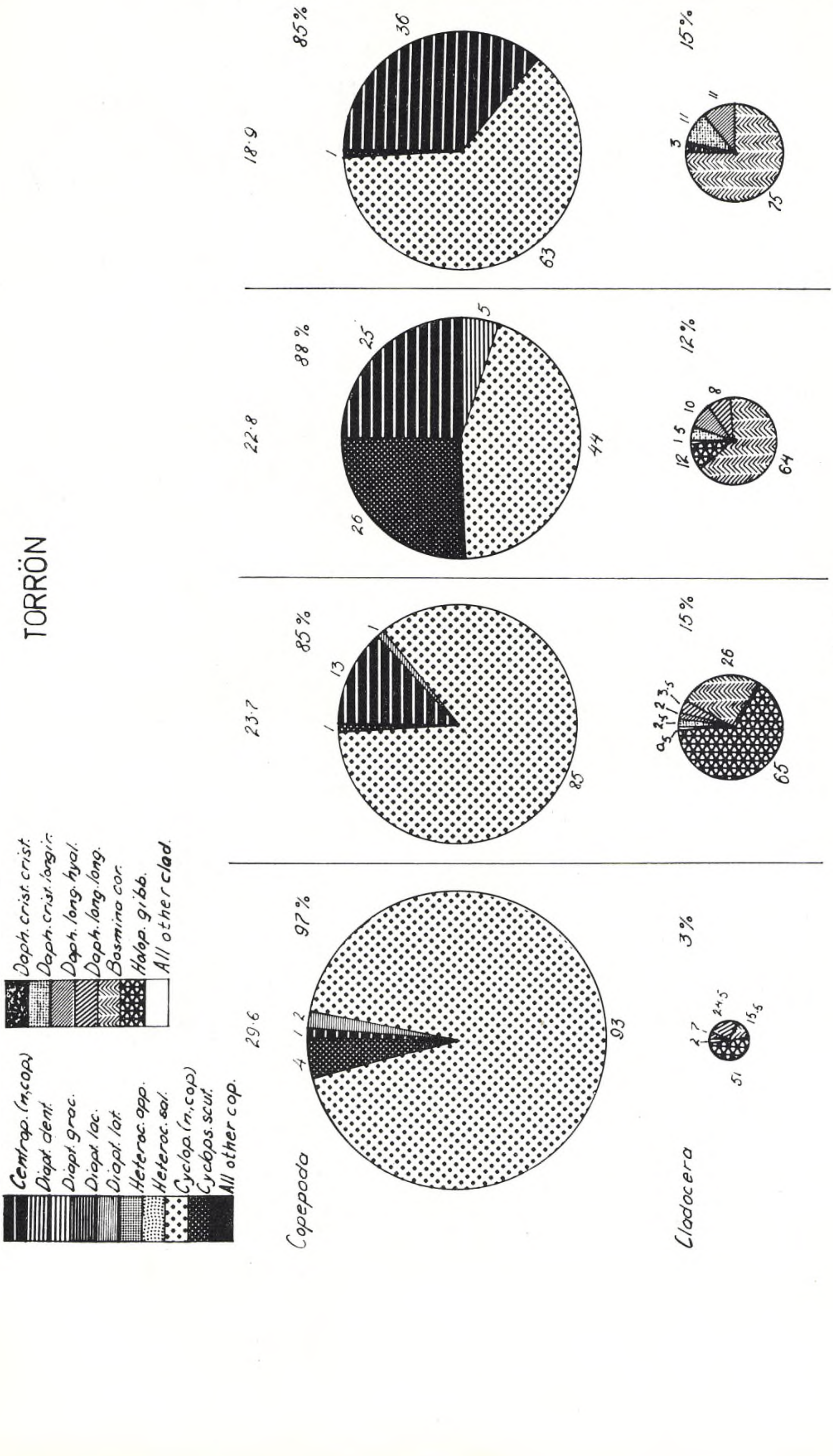
Diapt. grac.
Diapt. lac.
Diapt. lat.
Heteroc. app.
Heteroc. sal.
Cyclop. (n,cop.)
Cyclops. scut.
All other cop.
Daph. crist. crist.
Daph. crist. longir.
Daph. long. hyal.
Daph. long. long.
Bosmina cor.
Holop. gibb.
All other clad.
Copepoda
Cladocera
23.6
96%
67
33
46%
47
1
4
52
13.7
90%
59
1
39
10%
75
11
23
9.8
25%
59
8
21
1
11
75%
3
12
85
8.9
43%
35
14
4
1
46
57%
8
4
88

Fig. 28.


TORRÖN
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Diapt. dent.
Diapt. grac.
Diapt. lac.
Diapt. lat.
Heteroc. app.
Heteroc. sal.
Cyclop. (n, cop.)
Cyclops. scut.
All other cop.
Daph. crist. crist.
Daph. crist. longir.
Daph. long. hyal.
Daph. long. long.
Bosmina cor.
Holop. gibb.
All other clad.
Copepoda
Cladocera
29·6
97%
3%
23·7
85%
15%
22·8
88%
12%
18·9
85%
15%

Fig. 29.

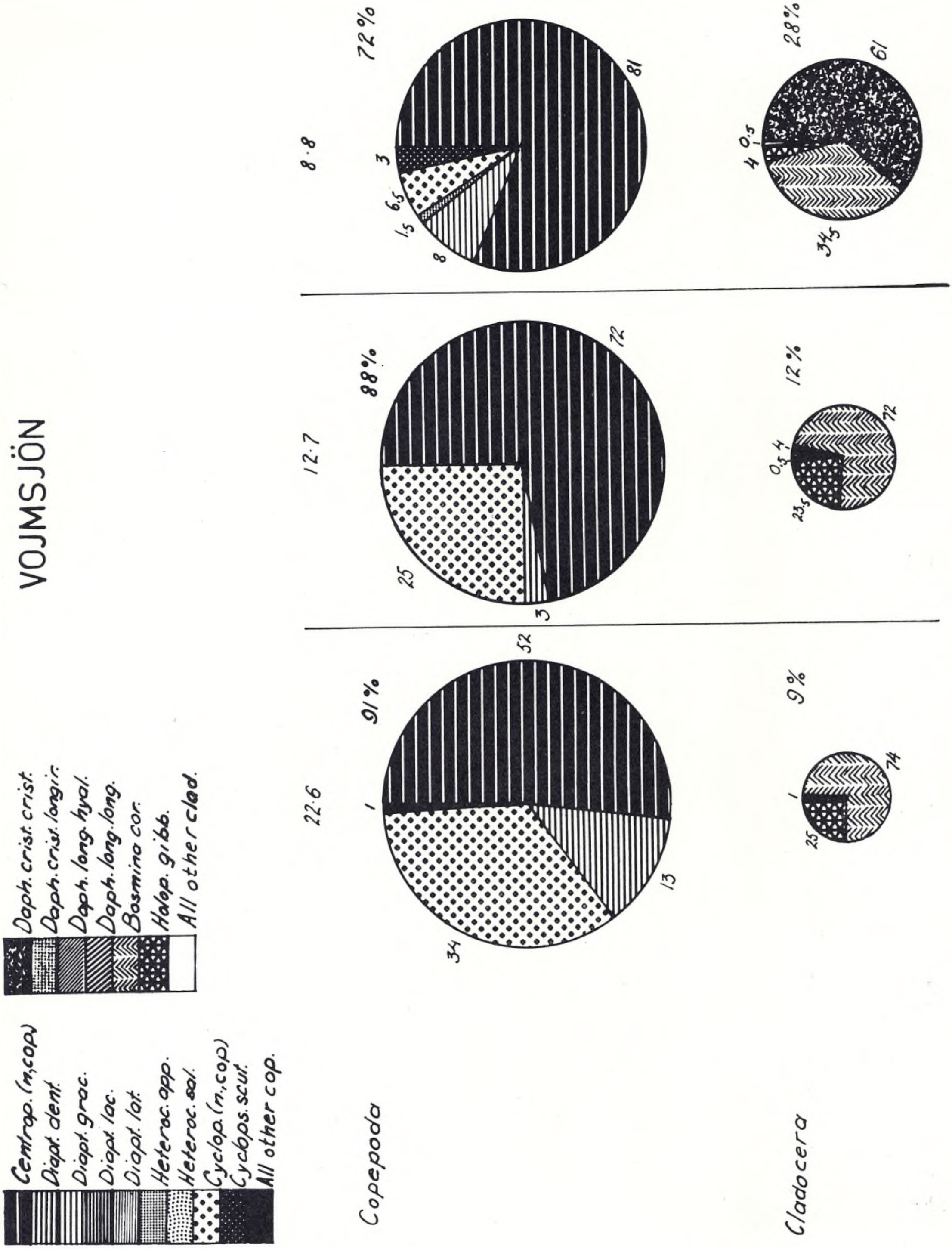
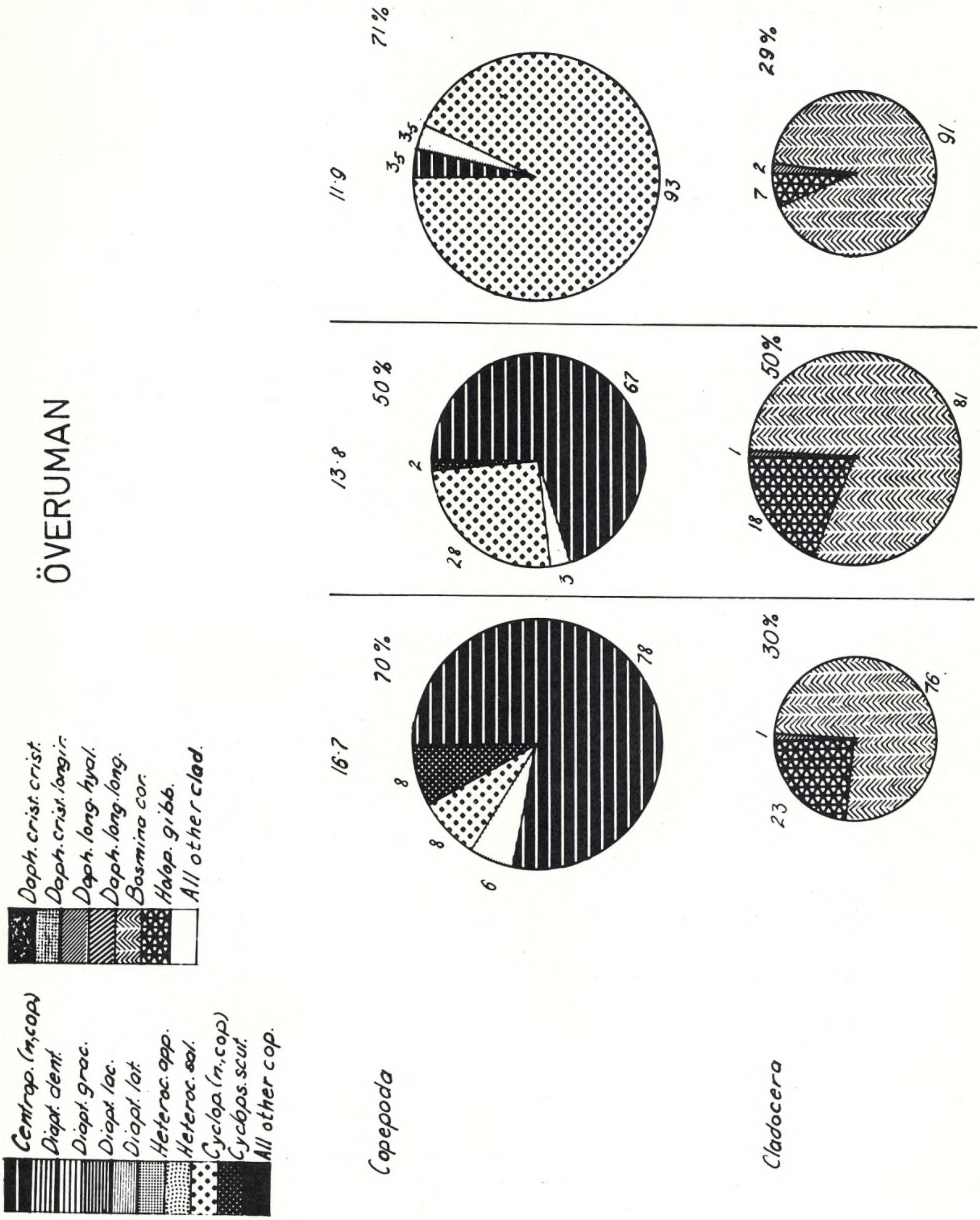

VOJMSJÖN
Centrop. (n.,cop.)
Diapt. dent.
Diapt. grac.
Diapt. lac.
Diapt. lat.
Heteroc. app.
Heteroc. sal.
Cyclop. (n.,cop.)
Cyclops. scut.
All other cop.
Daph. crist. crist.
Daph. crist. longir.
Daph. long. hyal.
Daph. long. long.
Bosmina cor.
Holop. gibb.
All other clad.
Copepoda
Cladocera
22·6
91%
1
52
13
34
9%
1
74
25
12·7
88%
72
25
3
12%
72
0.5
4
23.5
8·8
72%
81
3
6.5
1.5
8
28%
61
0.5
4
34.5

Fig. 30.


ÖVERUMAN
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Diapt. dent.
Diapt. grac.
Diapt. lac.
Diapt. lat.
Heteroc. app.
Heteroc. sal.
Cyclop. (n, cop.)
Cyclops. scut.
All other cop.
Daph. crist. crist.
Daph. crist. longir.
Daph. long. hyal.
Daph. long. long.
Bosmina cor.
Holop. gibb.
All other clad.
Copepoda
Cladocera
16·7
70%
78
8
8
6
30%
76
1
23
13·8
50%
67
2
28
3
50%
81
1
18
11·9
71%
3,5
3,5
93
29%
91
7
2

Fig. 31.

Studies on fish mortality due to passage through turbines

Preliminary report

By Erik Montén

With the introduction of the first Kaplan turbines European fishery officials and biologists began to take a serious interest in the injuries to fish passing through turbines. The first Swedish investigation was carried out by Alm (1927) with Lawaczeck turbines. Since then the importance of this question has increased in all countries where the power industry have had the opportunity to exploit rivers. At the end of the 1940's preparations began to be made in Sweden to use the head of rivers more intensively right to the river mouths.

So far as the river system had source lakes suitable for eel or intact nursery grounds for salmon and sea trout in the upper regions it was necessary to investigate the possibilities of smolt and adult eel passing power stations and reaching the coast alive.

Tests with special experimental turbines 1952—53

In 1952 the author started a series of investigations in order to assess the mortality of smolt in a large Francis turbine that had been planned. Living fish were dropped through model turbines, one Kaplan and one Francis, both installed at Motala Power Station with a head of 14.6 m. The Kaplan runner had a diameter of 600 cm and 6 vanes and the Francis 675 cm and 18 vanes. In all about 3,150 fish in 60 different series passed through the turbines and were recaptured in a funnel shaped net attached to the mouth of the draft tube. On average 92 % of the fish were recaught in the net. The condition of the fish before and after the tests was studied and compared with control groups. Test and control fish were transported by car 900 km from a fish-rearing plant. During one of the fish transports a stress effect caused solely by vibrations in the tank was established. The stressed fish showed an abnormally high mortality (about 70 % more than normal fish). The stress effect was obviated by changing the tank.

Both turbines were tested under normal runner speed and with varying gate openings (load). In other series the runner speed also was varied.

All recaptured injured fish were transilluminated or dissected and the features of interest were sketched and mapped. Internal changes were described.

At the tests at Motala several fish species were used, viz. salmon (*Salmo salar* L.), minnow (*Phoxinus phoxinus* (L.)), ide (*Leuciscus idbarus* (L.)), perch (*Perca fluviatilis* L.), pike (*Esox lucius* L.) and sticklebacks (*Gasterosteus*). The size of the fish ranged from about 4 cm up to 31 cm.

The author had the opportunity to modify the Francis turbine in such a way that the clearance between the guide vanes and the edge of the runner vanes was reduced. In spite of the reduction the interspace still exceeded the thickness of the fish. The changed interspace had no significant influence on the mortality.

To study the orientation of the passing fish the vanes of the Kaplan runner were provided in two tests with sharp knives covering in one test a peripheral and in the other a central portion of the edges. The material demonstrated that the longitudinal axes of the fish in a Kaplan turbine are only to a certain percentage orientated parallel to the stream direction. If the length of the fishes was twice that of the gate opening, about 50 % diverged from the stream direction by less than 20° while the others diverged by from 20° up to 60°.

The distribution of the passing fish along the edges of the runner vanes could be approximately calculated thanks to the possibility of distinguishing the difference between injuries caused by the knives and those inflicted by the intact part of the vane edges. There was a slight tendency to a higher density towards the periphery, possibly caused by an increase of the specific weight of the fishes in connection with a compression of the air bladder.

Tests with fish and balsa boxes in Francis turbines 1954

In 1954 the author performed some tests in two power stations with a head of 57 m and 108 m respectively. Both stations had Francis turbines. At these tests living smolt enclosed in boxes of balsa wood were used, a method earlier used by CARLIN (1949—1951). Fishes taken out from mechanically undamaged boxes showed on examination no signs of injuries caused by pressure variations or cavitation. Comparative tests with boxes were later made at Motala and the material was used to work out the hit probability. The investigations of 1952—1954 are briefly described in the above-mentioned report (MONTÉN 1955).

Tests in Kaplan turbines with living fish 1960

In 1960 the Swedish State Fishery Board started a series of investigations with live eels through Kaplan turbines (SVENSSON 1960—1961). Eight power stations were tested. The author had the opportunity to collaborate with

Svensson in these experiments. At two of the plants salmon smolt and some other types of fish besides eel were put through the turbines.

Sometimes it proves difficult to determine whether a recaptured fish has been pressed by the turbine runner or by the trapping net. In connection with these experiments some tests were made in order to demonstrate the influence of the net on the recaptured fishes: A few minutes in the net generally led to serious and striking skin injuries. An attempt to find any coherence between the degree of slipperiness of the fish body and the character of the mechanical injuries gave no significant result.

The fish material from these experiments was manipulated, checked and described in the same manner as the material from Motala.

The relative velocity and the relative openings

Both the effect of the collision in itself between fish and runner edge and the pressure of the water stream against a hit fish increase with the relative speed of the water (and fish) towards the runner edge. At a load representing the best exploitation of the water the vane angle (at the edge) for all turbines is accordant with the direction of the water stream in relation to the vane (relative stream direction). The radially or axially (Francis or Kaplan respectively) directed velocity of the water is possible to compute for every degree of the load. Also the absolute runner speed can be reckoned for any point of the vane edge. The author has so far as possible procured relevant data from those Swedish turbines in which fish experiments are made. For each turbine the absolute water velocity has been devided in components directed tangentially and along the runner vane respectively (the velocity parallelogram). In this manner satisfactory values of the relative velocity and the free openings between the vanes perpendicular to the relative stream direction (relative openings) have been calculated. In 1955 the author established that a decreasing of the load in the Francis turbine at Motala from full to half load reduced the mortality of salmon fingerlings from 50 % to 7.5 %. There is a critical range of the relative speed below which there will be no mechanical injuries. From the lower limit up to the upper limit the mortality increases with increasing relative speed, but a further increase of relative speed in the main only influences the character of the injuries, the mortality being affected hardly at all. In 1955 the lower limit for salmon parr was estimated at less than 4 m/sec. The author has since processed a larger body of material. Diagrams of the critical ranges have been drawn for salmon parr and eel. The eel tolerates a higher relative speed than do the salmon. The critical range of the salmon parr is calculated at about 2 $^1/_2$—3 $^1/_4$ m/sec and of the eel at about 3 $^1/_2$—5 $^1/_2$ m/sec. von Raben (1957) has supposed that the lower limit of the critical range for eel would lie between 11 and 14 m/sec.

Of interest for this question are some laboratory experiments started by the author in 1952 in order to study the effect of the pressure of the water stream on small fishes in contact with a net screen of metal. The importance of light for the orientation capacity was also studied. 5 cm minnows (*Phoxinus*) got trapped against the screen already at 0.8 m/sec and the speed had to be reduced to 0.3 m/sec to permit the fish to escape from the screen. Fish pressed for about 2 min at 1.8 m/sec had serious gill injuries.

The character of the injuries

The whole material of investigated injuries has given a good view of the way in which injuries arise in turbines. In Kaplan turbines there are some typical injuries caused by the fish being pressed between the runner blade and the chamber wall. These examples are more common than corresponds to the distribution of the entering fish. The fish must have been transported by the centrifugal force from the moment they had contact with the runner.

A comparison of all injuries was given in 1955. It was established that every fish species had a typical figure of injuries, determined by the specific anatomy, structure and resistibility of the species. The parts most exposed to injury are the brain region, the gills and the fin rays. A typical deep fin fissure observed on perches in the median plane along the dorsal fin is caused by the body being crushed against the runner edge under the pressure.

The hit probability

The probability that a fish of a certain kind and size will be hit by the vane edge is mainly determined by the relative openings between the runner vanes and the average extent of the fish in a direction perpendicular to the vane areas and the relative water stream. This extent of the fish is determined both by chance and by the stream conditions at the wicket-gate apparatus. In the light of the results at Motala the average projected length is calculated for different legth classes of the fish species used. In so far as the turbine has bigger relative openings than the absolute length of the fish the hit-percentage curve will correspond to the relationship between the opening and the above-mentioned calculated length. However, in the range where the opening is the same as the total length of the fish the curve begins to assume a more asymptotic shape with regard to the shorter projections. One hundred per cent hit will be reached at a point where the opening roughly corresponds to the thickness of the fish.

Even with a relative speed above the critical range the mortality does not directly depend on the projected total length but on the projected vulnerable part of the fish. Considering the distribution of the injuries the vulnerable length has been estimated (especially for young salmon and adult eel) for relative velocities above the critical range. A smolt of 14.5 cm total length and an eel of 73.5 cm generally correspond to an average projected vulnerable length of 7—8 cm and 48 cm respectively.

Comparison between computed and practical results

The theoretical computed values have been compared with the author's and other published practical results. In particular the mortality values given in the older literature have been critically examined. For each fish species all values have been corrected to the same length and to a load corresponding to the same efficiency of the turbine. A very satisfactory agreement between these values and the theoretical values computed with regard to the hit probability and the relative speed has been established for all Kaplan (and Lawaczeck) turbines and for Francis turbines with low or moderate head. In regard to high-head turbines and turbines with the runner centre 4—5 m or more above the tail water level it is necessary — as has been shown in the U.S.A. (VON GUNTEN, CRAMER and OLIGHER 1960—63) — to count, especially in operations below and above the range of maximum efficiency, with an additional mortality caused by extra pressure changes in the cavitation regions.

The material collected or processed by the author will be exhaustively presented and illustrated with diagrams in a future issue of this publication.

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The occurrence of terrestrial insects on the surface of two lakes in northern Sweden (Ankarvattnet and Blåsjön)

By ÅKE NORLIN

Institute of Zoology, Entomological Department, Uppsala

Introduction

Extensive investigations carried out with regard to changed feeding habits of fishes in connection with artificial water level fluctuations have shown, among other things, the increased importance of terrestrial insects as food for fish in regulated lakes (NILSSON 1961).

Large temporary accumulations of such insects are often referred to in the daily press as a "rain of insects", and minor notes on such occurrences also find their way into the entomological journals.

The phenomenon as such has been studied by entomologists from the point of view of dispersal ecology. In this connection the term "anemohydrochorous spreading of insects" has been created. This phenomenon has been exhaustively studied by PALMÉN (1944). PALM (1933, 1949) has observed cases of such spreading of insects in the Swedish lakes Vättern and Torne Träsk.

The aim of the present investigation has been to find out the main components and the origin of the terrestrial insect fauna appearing on the surface of some north Swedish lakes.

Methods

During the summer of 1962 the field work was located at the neighbouring lakes of Blåsjön and Ankarvattnet in Jämtland, northern Sweden. The distance between the lakes is about 3 km. The climate and the physico-chemical properties of the waters are closely similar (GRIMÅS 1961). In Lake Blåsjön a water-level regulation for hydro-electric purposes took place in 1947.

In both lakes the sampling was carried out mainly at two fixed stations. These were situated along the western shores of the lakes and exposed to the dominant directions of the wind, where the greatest accumulations of drifted animals could be expected. In Lake Blåsjön one of the stations was situated outside a cultivated area (B 1), while the other was adjacent to an area covered with conifers (B 2). The latter also applied to one station in Ankarvattnet (A 2), while the other bordered on to a region with birch, alder, and a rich ground flora (A 1). In addition to this, random samples were taken in the open water and at different parts of the shore of both lakes.

In order to permit comparison of material from different localities, the samples were collected from the surface of the water immediately off the shoreline. Collecting was carried out with a long-handled net with square frame, the sides of which were one third of a metre long. The bag was made of fine-mesh nylon tulle. This net was moved once over a measured distance of 100 metres for every quantitative sampling.

In addition to the sampling in the water surface, samples were collected with a sweeping net in the surrounding shore biotopes.

Material

The material collected from the water surface amounts to 100 samples with altogether 3,267 insects distributed over 11 orders. The material from shore biotopes is of about the same magnitude.

Table 1 shows the total distribution of animals over different orders and the percentage formed by each order in the number of the total catch. This table also includes a factor of constancy, i.e. the percentage among all samples of those containing a certain group of species (cf. TISCHLER 1949, p. 8, ODUM 1960, p. 382). All insects caught in the net were reported, including those who have their natural environment in the water surface or pass through it after their larval development within the lake. For this reason the latter constitute a large percentage of the catch, especially among the *Diptera*. Their inclusion is due to the desire to give a comprehensive picture of the composition of what is here called the surface fauna. Thus the surface fauna is considered to consist partly of animals that are involuntarily retained by the surface tension and are carried passively by winds and currents, and

Table 1. Total distribution over different orders of insects collected from the surface of Lakes Blåsjön and Ankarvattnet in 1962.

Order	Factor of constancy	Number of animals	Percentage of the total number
Collembola	12	12	0.37
Ephemeroptera	12	42	1.29
Plecoptera	15	34	1.04
Psocoptera	6	16	0.49
Hemiptera	60	334	10.22
Coleoptera	65	328	10.04
Hymenoptera	79	775	23.72
Trichoptera	19	23	0.70
Lepidoptera	19	24	0.73
Mecoptera	1	1	0.03
Diptera	91	1,678	51.36

Table 2. Families of insects occurring on the surface of Lake Blåsjön between June 14 and October 13, 1962.

	Regular	Occasional	
Hemiptera	*Euscelidae* *Aphididae*	*Heteroptera* sp. *Araeopidae* *Cercopidae*	*Typhlocybidae* *Psyllidae*
Coleoptera	*Staphylinidae* *Cantharidae*	*Carabidae* *Dytiscidae* *Scarabaeidae* *Hydrophilidae* *Liodidae* *Nitidulidae* *Erotylidae* *Colytidae*	*Coccinellidae* *Byrrhidae* *Elateridae* *Chrysomelidae* *Cerambycidae* *Curculionidae* *Scolytidae*
Hymenoptera	*Ichneumonidae* *Braconidae* *Chalcididae*	*Tenthredinidae* *Pamphilidae* *Proctotrupidae*	*Cynipidae* *Formicidae*
Diptera	*Tipulidae* *Chironomidae* *Bibionidae* *Mycetophilidae* *Empididae* *Phoridae* *Lauxaniidae* *Agromyzidae* *Ephydridae* *Muscidae*	*Anisopodidae* *Psychodidae* *Ceratopogonidae* *Simulidae* *Scatopsidae* *Cecidomyiidae* *Stratiomyiidae* *Rhagionidae* *Tabanidae* *Asilidae* *Dolichopodidae*	*Pipunculidae* *Syrphidae* *Psilidae* *Platystomidae* *Trypetidae* *Sepsidae* *Sciomyzidae* *Helomyzidae* *Borboridae* *Chloropidae* *Calliphoridae*

partly of the *neuston* (cf. Odum 1960 p. 295) which have their natural environment on the surface. The former part of the surface fauna is here called "drifting fauna" (cf. Rapopórt and Sánchez 1963 p. 98).

The factors of constancy show that the orders represented can be divided into two groups. *Collembola, Ephemeroptera, Plecoptera, Psocoptera, Trichoptera, Lepidoptera,* and *Mecoptera* exhibit constancies below 20 per cent, while the orders *Hemiptera* (including *Heteroptera* and *Homoptera*), *Coleoptera, Hymenoptera,* and *Diptera* have constancies of 60 per cent or more. Since the four last-mentioned orders furthermore represent 95 per cent of the total number of the catch, there are good reasons for disregarding the first-named group for the time being.

The four orders treated have been classified to the family level. This classification is summarized in Table 2, where also a division has been carried out into regularly- and occasionally-appearing families. Families which have constancy greater than 20 per cent and which form more than 2 per cent of the total material have been regarded as regularly-appearing. This limit is of course open to discussion, but in practice leads to a selection of the most important groups.

Results

Table 3 gives a comparison between the dominating families of insects found in stomach contents of fishes investigated by NILSSON (1955, 1961), and the occurrence of these families on the water surface of Lake Blåsjön in 1962. There is a good correspondence between the compared material. All the insect groups mentioned as dominating by NILSSON are found within the four most frequent orders of insects dealt with in this investigation. An exception is *Oporinia autumnata*. This species of *Lepidoptera* occurred in 1954 in very great masses and then periodically formed a dominating part of the fish food, while in 1962 this species occurred very sparsely. A few families, especially within the *Diptera,* with regular occurrence in the material of the present investigation, are not mentioned by NILSSON. This seems to be due to the fact that NILSSON has not classified parts of his material to family level, but has reported it under headings of higher systematic rank, e.g. *Diptera sp.*

Among the families that regularly appear in the collected material we find several which on account of their biology are directly linked with the water, viz. *Tipulidae, Chironomidae* and types of *Empididae* and *Ephydridae*. These have, therefore, strictly speaking, no place within the frame of this investigation, but when my attention had been directed to the occurrence of the fam.

Table 3. Dominating groups of insects caught by fish 1948, -49, -54, -56 and -59 compared with the occurrence of the same groups on the water surface in 1962; (Reg=regular, Occ=occasional).

	Caught by fish	Occurrence 1962
Hemiptera	*Aphididae*	Reg
	Psyllidae	Occ
	Jassidae	No
Coleoptera	*Carabidae*	Occ
	Staphylinidae	Reg
	Scarabaeidae	Occ
	Ipidae	No
	Cantharidae	Reg
	Elateridae	Occ
	Chrysomelidae	Occ
Hymenoptera	*Tenthredinidae*	Occ
	Ichneumonidae	Reg
	Cynipidae	Occ
	Formicidae	Occ
	Apidae	No
Diptera	*Bibionidae*	Reg
	Mycetophilidae	Reg
	Phoridae	Reg
Lepidoptera	*Oporinia autumnata*	Occ

Tipulidae (GRIMÅS 1961), I noticed an obvious difference between the investigated lakes.

	Number of collected *Tipulidae*	Constancy per cent
Blåsjön, station 1	26	46
,, ,, 2	31	44
Ankarvattnet, station 1	1	7
,, ,, 2	0	0

A rich occurrence of tipulids was observed within the regulated zone not only in Lake Blåsjön but also in the regulated arctic Lake Semmingsjön, east of Blåsjön. It seems that a periodic exposure of large areas of the bottom of the lakes favours the production of these animals.

Among the purely terrestrial groups in the material, many have proved to have their most important natural habitat in regions with deciduous forest and rich vegetation of herbs, fewer of them in regions with coniferous forest. This can be exemplified by types among the families *Euscelidae, Aphididae, Cantharidae, Chalcididae, Bibionidae, Agromyzidae,* and *Muscidae.*

In principle the lakes receive their supply of drifting material in two ways, viz. partly by the downfall of insects floating high up in the air, so-called "aerial plankton" (cf. ALLEE et al. 1950, p. 148), partly by downfall of insects dispersing from neighbouring shores. The mass of insects floating in the air can occasionally be considerable (ALLEE et al. 1950, p. 150). Under certain meteorological conditions fallen aerial plankton will certainly form a considerable proportion of the mass of drifting fauna. This is the case, e.g., in certain noticed instances of a "rain of insects" (PALM 1933, 1949). During this investigation there was no occurrence on the water surface of such large numbers of insects as to justify one in speaking of a "rain of insects".

With the aim of forming an idea about the importance of different modes of supply, samplings were carried out at different distances from the shore. On these occasions there was only a very slight wind or none at all. As an example the results of July 30, 1962, are given. The volumes have been obtained by measurement with a burette graduated in 0.05 ml.

Distance	Volume of catch	Numbers of families	Numbers of individuals
0—100 m from shore	0.45 ml	19	60
2—300 ,, ,, ,,	0.10 ml	8	11
4—500 ,, ,, ,,	0.05 ml	7	9

Similar results were obtained on other occasions. This indicates that the greater part of the drifting fauna under the conditions mentioned descends onto the water surface from the surrounding shores.

Table 4. Samplings at the fixed stations in Lakes Blåsjön and Ankarvattnet June 14—August 13, 1962.

	Station	Number of samples	Number of pos. samples	Number of individuals	Number of individuals per sample	Constancy
Hemiptera	B 1	11	8	58	5.3	73
	B 2	10	6	72	7.2	60
	B 1 and 2	21	14	130	6.2	67
	A 1	14	6	24	1.7	43
	A 2	13	7	24	1.8	54
	A 1 and 2	27	13	48	1.8	48
Coleoptera	B 1	11	8	68	6.2	73
	B 2	10	8	83	8.3	80
	B 1 and 2	21	16	151	7.2	76
	A 1	14	10	28	2.0	71
	A 2	13	6	12	0.9	46
	A 1 and 2	27	16	40	1.5	59
Hymenoptera	B 1	11	10	118	10.7	91
	B 2	10	9	157	15.7	90
	B 1 and 2	21	19	275	13.1	90
	A 1	14	9	47	3.4	64
	A 2	13	10	119	9.2	77
	A 1 and 2	27	19	166	7.9	70
Diptera	B 1	11	11	206	18.7	100
	B 2	10	8	274	27.4	80
	B 1 and 2	21	19	480	22.9	90
	A 1	14	11	72	5.1	79
	A 2	13	11	89	6.8	85
	A 1 and 2	27	22	161	6.0	81

The column "Number of pos. (positive) samples" indicates how many times animals of the order in question occurred in samples.

The stations in Lake Blåsjön are denoted by the symbols B 1 and B 2, those in Ankarvattnet by A 1 and A 2.

Table 5. Samplings at the fixed stations in Lake Blåsjön June 14—October 13, 1962.

	Stations	Number of samples	Number of pos. samples	Number of individuals	Number of individuals per sample	Constancy
Hemiptera	B 1	26	16	79	3.0	62
	B 2	25	15	140	5.6	60
Coleoptera	B 1	26	17	84	3.2	65
	B 2	25	18	123	4.9	72
Hymenoptera	B 1	26	22	181	7.0	85
	B 2	25	22	287	11.5	88
Diptera	B 1	26	26	701	27.0	100
	B 2	25	23	676	27.0	92

Tables 4 and 5 contain an account of samplings at the fixed stations in Lakes Blåsjön and Ankarvattnet, and of the numbers of caught animals belonging to the four main orders. The numbers expressing constancy and the ratio individuals per sample can serve for a comparison between the lakes and between their respective stations. Owing to the fact that in Ankarvattnet the sampling was terminated on August 13, while in Blåsjön it continued to October 13, the results are presented in two tables in order to make possible a comparison of the figures. Thus Table 4 comprises both Blåsjön and Ankarvattnet for the period June 14—August 13, while Table 5 covers the two stations in Lake Blåsjön during the entire sampling period from June 14 to October 13.

Differences between the lakes

Table 4 shows that Lake Ankarvattnet is inferior to Lake Blåsjön especially with regard to the ratio individuals per sample, but also with regard to constancy. In spite of the many similarities between the lakes (GRIMÅS 1961) some differences that are of importance for the present results can be pointed to, quite apart from the fact that Lake Blåsjön has been affected by water-level regulation for about 15 years:

1. Lake Blåsjön covers 39.96 km^2, while the area of Lake Ankarvattnet is only 9.34 km^2. Lake Blåsjön therefore receives a greater number of wind-driven insects than does Ankarvattnet, probably both by the downfall of insects floating high up in the air and by emigration from the shores. The drift gathered in this way in the water surface is not stationary, but is assembled by the wind in relatively narrow drift lines off the wind-exposed shore. Sampling at the stations along these shores therefore gives a greater total catch in Blåsjön and produces the impression that the surface of this lake contains a greater number of terrestrial insects per area than does Ankarvattnet.

2. There is a difference in "gathering capacity" between the shores at the fixed stations in the lakes. The term "gathering capacity" is used for the ability of a stretch of shore to retain drifting material outside it. This ability is conditioned by currents and wind directions, and also by the configuration of the shoreline. Part of the material cast upon a flat shore is hidden among stones and non-animal drift and a large proportion of the drifted fauna can also take to their wings as soon as they have become dry. Off steep shores, on the other hand, the animals are retained until they sink. Small bays and creeks of comparatively unruffled water often contain great masses of drifting material. Incoming water continuously brings along additional material which accumulates on the water surface and is not driven below it or carried away again by countercurrents.

The western shore of Lake Blåsjön is much steeper than that of Ankarvattnet. Thus the stations of Lake Blåsjön have greater gathering capacity than those of Ankarvattnet.

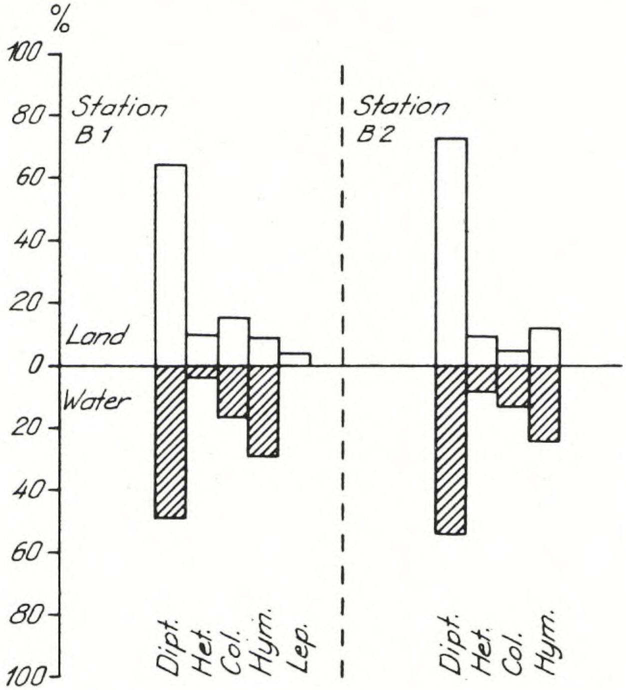

Diagram comparing the distribution over the main orders of the material collected during July 1962 at stations B 1 and B 2, and corresponding shore biotopes.

Consequently the differences in the gathering area and gathering capacity of the two lakes may explain why the mass of drifting fauna sampled from Lake Blåsjön is greater than that from Lake Ankarvattnet. It can, however, be considered essential that the actual difference in content of this material does not indicate any difference to the disadvantage of the regulated lake.

Differences between the fixed stations

At the two stations in Lake Blåsjön the differences between the figures for individuals per sample and for constancy may be covered by random variations (Table 5). The stations are similar with regard to gathering capacity and to the area of the water surface from which they have received their drifting material. Station B 1 is, however, situated outside a cultivated area, while station B 2 is adjacent to an area covered with conifers. If most of the insects in the water surface have descended onto it from the neighbouring shores (cf. p. 200), there ought to be a great similarity between the specific composition of the insect fauna on the stations and the corresponding shore biotopes.

Diagram p. 203 gives a comparison of the distribution over the main orders of the material collected during July 1962 at the stations B 1 and B 2, and the shore biotopes bordering on these stations.

There is obviously a good correspondence between the distribution of these orders on the two stations in water, whereas the correspondence in the material from the two biotopes on the shore is not so good. Unexpectedly the agreement is less good on comparison between the shore biotope and the water surface at the respective stations. A study of the composition of families within the orders reveals that some families have a good correspondence between their occurrence on land and water respectively, e.g. *Empididae, Agromyzidae, Muscidae* and *Cantharidae.* On the other hand the fam. *Bibionidae,* e.g., constituted 25 per cent of the material from the shore at station B 2 during the period mentioned above, while the corresponding percentage in the material from the water surface was 5. The group *Parasitica,* mostly small specimens, constituted during this time 28.0 (B 1) and 17.5 (B 2) per cent, respectively, of the insects on the water surface, but only 3.2 and 6.0 per cent respectively of those on the shores. Similar were the conditions among, for instance, the fams. *Staphylinidae* and *Tenthredinidae.*

It is obvious that the similarities that ought to be found between the insect fauna in the water surface and the shore biotope at the same station and the difference that ought to exist between stations in the water owing to different bordering shore biotopes have been overshadowed by some other factors determining the distribution of drifting fauna.

One of these factors might be the downfall of aerial plankton. The rather frequent occurrence of, for instance, small *Parasitica* indicates that this factor is of a certain importance. Of greater importance is the mobility of the surface fauna. As soon as a slight wind rises, the fauna is gathered in stripes and carried towards the exposed shore. According to calculations by BIGLOW and EDMONDSSON (1947), the speed of movement of the surface water amounts to about two per cent of the existing velocity of the wind. The drift which rises above the surface and thus also catches the wind must move at at least the same speed. Since Blåsjön is about 8 km across at its widest point, the foregoing implies that at a wind velocity of 5 m/sec the drift can be carried from one shore to the other in less than 24 hours. In consequence of this, sampling on leeward shores always gave a very poor catch of drifting insects.

Finally, it can be said that the particular form of fish food discussed here seems to spread onto the water surface of the lake from different parts of the shore in a similar degree. This mass of floating insects, however, accumulates rather quickly against the windward shore. In part this drifting fauna is cast upon the shores and is then no longer available as fish food, but considerable portions of it are carried to steep parts of the shore with great gathering capacity where it is retained outside the shoreline, available for the fish for a fairly long period.

Summary

1. In the summer of 1962 the appearance of terrestrial insects on the water surface was examined in Lakes Blåsjön and Ankarvattnet in northern Sweden. The collected material, consisting of 3,267 insects distributed over 11 orders, was classified to the family level.
2. The order *Diptera,* followed by the orders *Hymenoptera, Heteroptera,* and *Coleoptera,* dominated the material.
3. Most of the drifting fauna on the surfaces of the lakes is probably derived from the surrounding shore regions and only to a smaller degree by the downfall of "aerial plankton".
4. Existing differences between the examined lakes are presumed to depend on differences in the areas of the lakes and in the gathering capacity of the shores.
5. Sampling off shores with different kinds of vegetation showed very small differences owing to the fairly fast transport and mixing of the drift on the whole water surface.

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Influence of low temperature on the blood lactate level in *Salvelinus fontinalis* after exercise

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Several authors have showed that hard muscular exercise in fish results in a marked rise in blood lactate (Secondat and Diaz, 1942; Black, 1955, 1957 a, b, c; Nakatani, 1957; Parker and Black, 1959; Heath and Pritchard, 1962). In mammals also there is an increase in blood lactate after hard exercise (Bang, 1936; Andersen et al., 1960). There is, however, a difference of great interest between mammals and fish. In mammals resting level is again reached 60—90 minutes after exercise (Bang, 1936; Andersen et al., 1960) but in fish the changes are much slower and the pre-exercise level is seldom reached until the 8th—24th hour of recovery (Black, 1957 a, b, c; Black et al., 1959, 1960).

The present experiments were undertaken to obtain data on the influence of low temperature on the accumulation and disappearance of lactate in fish blood after exercise and are included in a larger investigation concerning a wide range of temperatures. Although different workers have investigated the lactate accumulation at different temperatures (Black, 1955, 1957 a, b, c; Nakatani, 1957; Parker and Black, 1959; Heath and Pritchard, 1962), a systematic investigation of the temperature effect covering the whole range from 0—20°C is still lacking.

Material and methods

Speckled trout, *Salvelinus fontinalis,* were obtained from a local hatchery, 1-year-old during spring 1962, 1 1/2-year-old during autumn 1962 and 2-year-old during winter 1963. All were from the same hatching. They were kept in aquariums (400 l.) in dechlorinated running tap water for at least 3 weeks before using and were fed horse liver each afternoon except on the day of the experiment.

The exercise was carried out by chasing the fish for 15 minutes in a plastic trough filled with dechlorinated running tap water. The recovery took place in a "respirometer", through which the water was circulating and where air and water were mixed in a mixing chamber. The apparatus, mounted on a "Perspex" plate was immersed in a thermostatically controlled waterbath (±0.5°C). Thus exercise and recovery took place in different containers. The transfer took a minimum of time (about 5 sec.), and there was the same quality of water in both containers. Blood was drawn from the heart of the lightly anaesthetized fish into a heparin-rinsed syringe. The anaesthetic used was a 1 : 12000 solution of M.S. 222 (tricaine methanesulphonate, Sandoz). This anaesthetic is not entirely satisfactory as it may cause circulatory and respiratory changes (RANDALL, 1962), but in this case the anaesthetizing never took more than 90 sec., and permitted handling with a minimum of struggling. The time required to obtain the blood sample was from 30 to 120 seconds. Groups of fishes were blood-sampled after exercise and at different times during recovery. Blood was taken only once from each fish. In 1962 lactate content was estimated according to Barker-Summerson (COLOWICK and KAPLAN, 1957) and in 1963 according to a modified microdiffusion method (CONWAY, 1957; SCHOLANDER and BRADSTREET, 1962). A comparison revealed no difference between the results of the two methods. The latter method is to be preferred because it requires only very small blood samples (down to 5 mm^3) and is not so time-consuming.

A modified Winkler method was used for the estimation of dissolved oxygen (KROGH, 1935). The pH was measured potentiometrically with glass electrodes.

Results

A. *Behaviour during exercise*

Temp. 15°C. Spring 1962.

All the fish were considered to be in an "unexercised" condition before exercise. After 3—5 minutes of exercise the first sign of fatigue was seen. The fishes were no longer swimming away from the source of stimulation. If permitted, they would stop swimming and rest on the bottom, usually in the darkest corner. At the end of the exercise the fishes, almost without exception, were exhausted. They lay motionless in the hand.

Temp. 5°C. Winter 1963.

The same behaviour was seen as is described above. (The impression was gamed, however, that for seasonal reasons, because they were winter animals, and/or owing to the low temperature the fish were inactive and not fully exhausted by exercise.)

B. *Influence of low temperature (5°C) on the accumulation of blood lactate*

As seen in Table I the obtained values were low compared with those at 15°C, (Table II), and there was no marked rise in blood lactate during recovery. A few experiments performed at a temperature of 11.5°C (O_2-satu-

Table I. Changes in blood lactate in mature *Salvelinus fontinalis* after 15 minutes' strenuous exercise and during 4 hours of recovery. Temp. 5°C, O_2-saturation 83—100 %, pH 7.1—7.5. Time of the year: Feb., March 1963. Total number of animals: 20. $\mathrm{S.D.} = \sqrt{\frac{S(x-\bar{x})^2}{n-1}}$

	Exercise	Recovery		
	15 min.	1 hour	2 hours	4 hours
Number of animals (n)	5	5	5	5
Body				
Weight (grams)				
Mean ± S.D.	193 ± 54	152 ± 18	151 ± 10	152 ± 23
Range	122—243	131—172	141—167	117—179
Blood				
lactate (mg %)				
Mean ± S.D.	28 ± 3	34 ± 13	35 ± 10	31 ± 14
Range	21—36	19—52	24—51	13—61

Table II. Changes in blood lactate in immature *Salvelinus fontinalis* after 15 minutes' strenuous exercise and after 2 hours of recovery. Temp. 15°C, O_2-saturation 85—98 %. Time of the year: May, June 1962. Total number of animals: 9. $\mathrm{S.D.} = \sqrt{\frac{S(x-\bar{x})^2}{n-1}}$

	Exercise	Recovery
	15 min.	2 hours
Number of animals (n)	5	4
Body		
Weight (grams)		
Mean ± S.D.	23 ± 8	26 ± 6
Range	19—37	18—33
Blood		
lactate (mg %)		
Mean ± S.D.	68 ± 21	118 ± 36
Range	36—82	98—166

ration 80—95 %; pH 7.1—7.4) during autumn 1962 on not quite mature 1 ½-year-old speckled trout (weight 143 ± 10 g) gave the mean value 109 ± 5 mg % (n = 5; range 104—114) after 2 hours of recovery.

Discussion

A marked finding was that the lactate level was low after exercise at 5°C. According to BLACK (1957 a) there was no difference in blood lactate level of yearling Kamloops trout after 15 minutes' vigorous exercise at 11.5°C and 20°C respectively. In the latter case the trout were acclimatized to 20°C. In the experiments here reported the seasonal variations in temperature were used. A confusing fact is that the low blood lactate level is obtained from fish in a mature stage, the higher lactate levels were obtained from fish in immature and not quite mature stages respectively. BLACK et al., (1960) showed that after exercise of wild mature spawning Kamloops trout the blood lactate level was lower than the levels obtained in 1 ½-year-old and 2-year-old hatchery-reared trout. In the present experiments, however, the three sets of fishes were from the same hatching, and diet, way of feeding and sampling time were the same in all instances. Unfortunately there was no opportunity to determine the level of muscle glycogen before and after the different experiments, because the fish were kept alive after blood sampling.

Further experiments require that the exercise shall be standardized and the fish be exercised to fatigue and recovered in the same container, keeping pH and contents of O_2 and CO_2 under exact control (BAZU, 1959). Other factors that have to be considered are age, sexual maturity, diet and physical training (MILLER et al., 1959 and HOCHACHKA, 1961).

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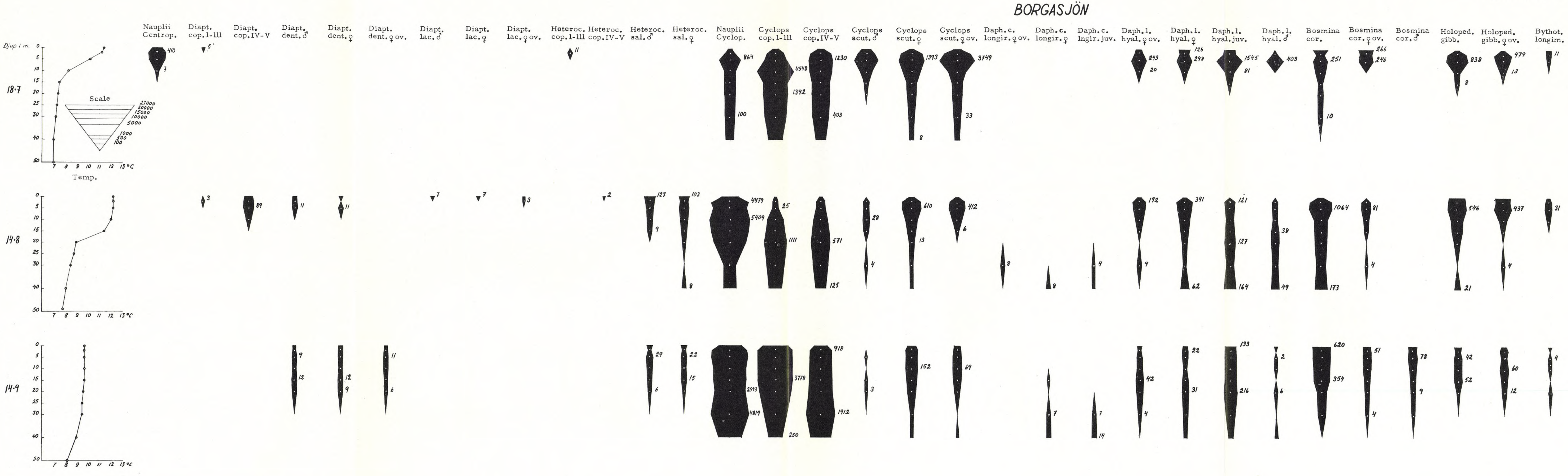
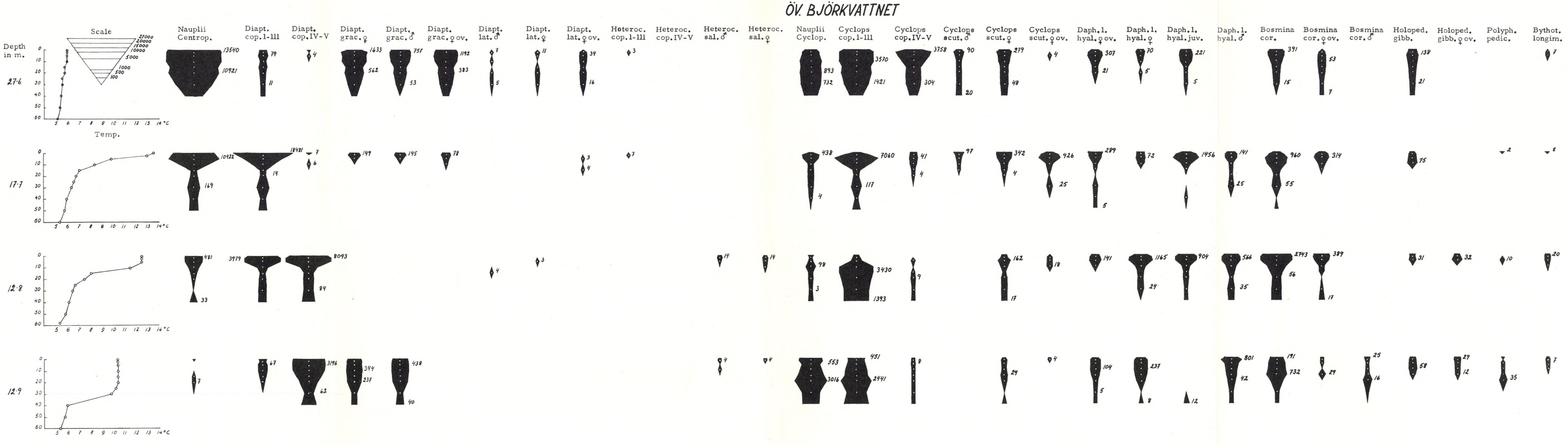
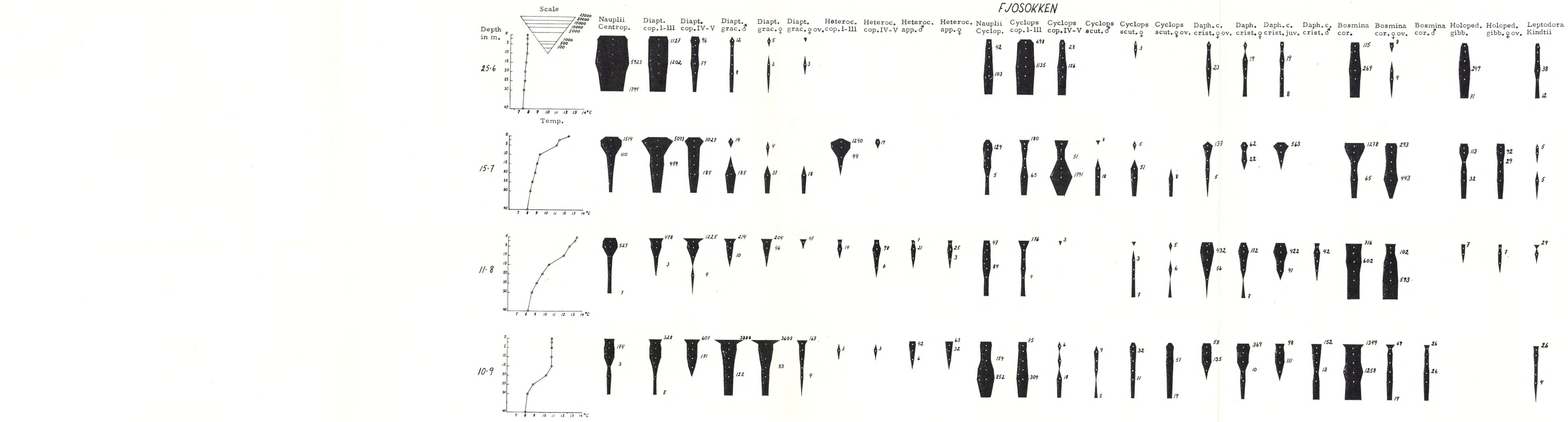
Appendix, fig. 32.



Lötmarker, Rept. Inst. Freshw. Res. Drottningholm, 45: 113—189.



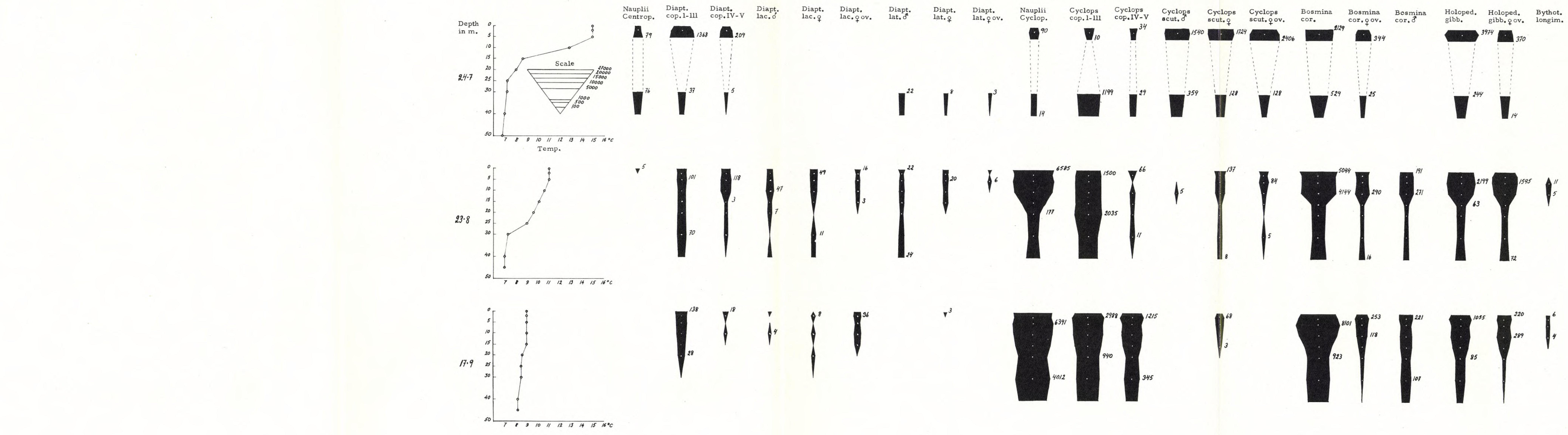
Lötmarker, Rept. Inst. Freshw. Res. Drottningholm, 45: 113—189.



Lötmarker, Rept. Inst. Freshw. Res. Drottningholm, 45: 113—189.

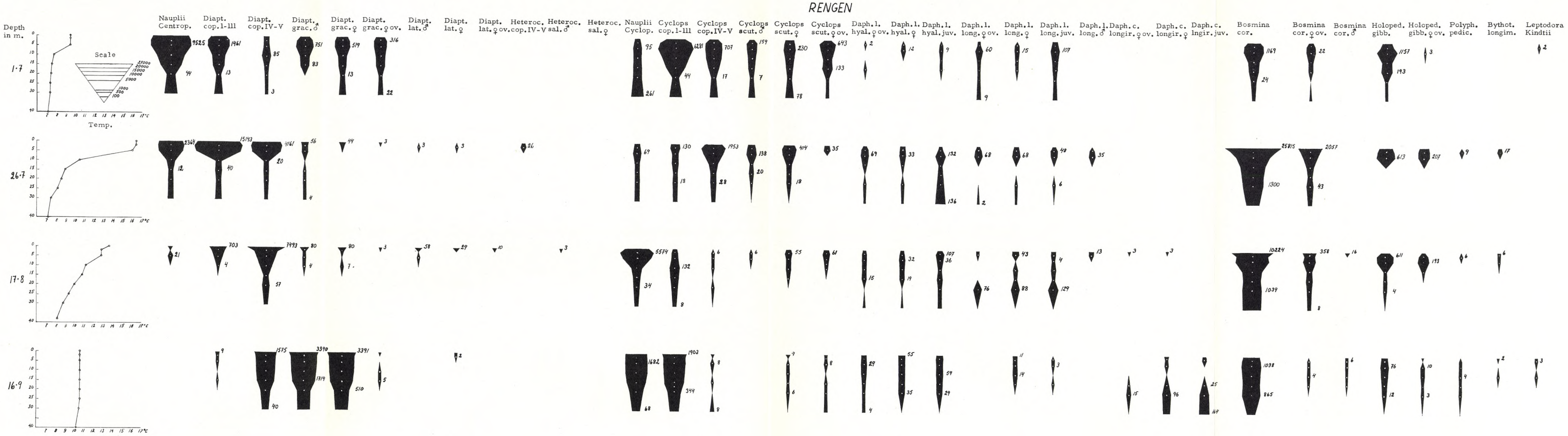
KVARNBERGSVATTNET

Lötmarker, Rept. Inst. Freshw. Res. Drottningholm, 45: 113—189.


ST. MJÖLKVATTNET
Depth in m.
Scale
Temp.
°C
24·7
23·8
17·9
Nauplii Centrop.
Diapt. cop. I-III
Diapt. cop. IV-V
Diapt. lac. ♂
Diapt. lac. ♀
Diapt. lac. ♀ ov.
Diapt. lat. ♂
Diapt. lat. ♀
Diapt. lat. ♀ ov.
Nauplii Cyclop.
Cyclops cop. I-III
Cyclops cop. IV-V
Cyclops scut. ♂
Cyclops scut. ♀
Cyclops scut. ♀ ov.
Bosmina cor.
Bosmina cor. ♀ ov.
Bosmina cor. ♂
Holoped. gibb.
Holoped. gibb. ♀ ov.
Bythot. longim.

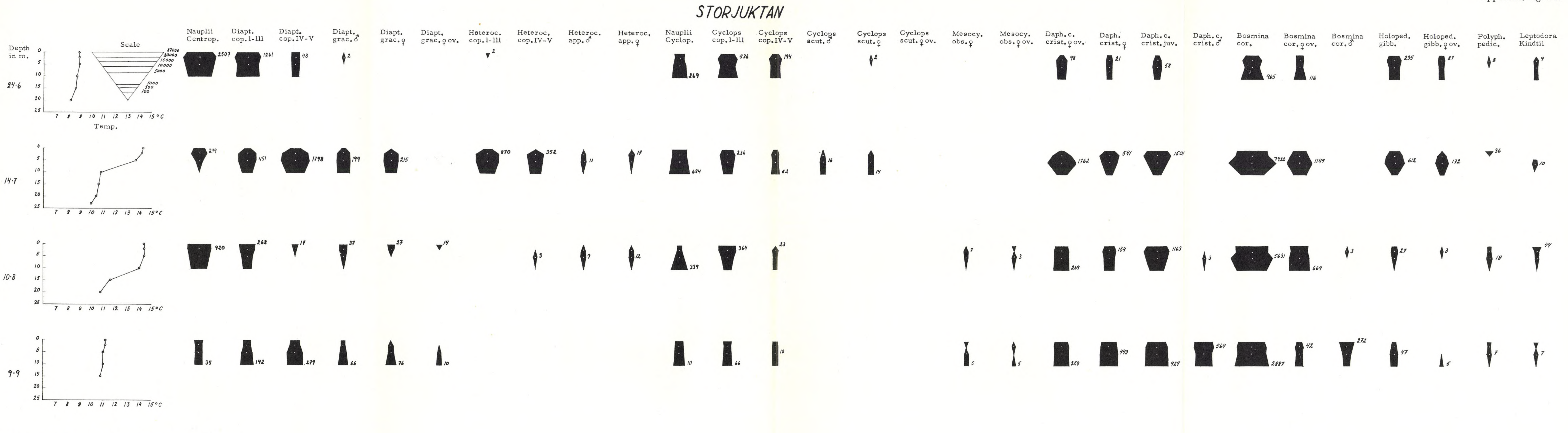
Lötmarker, Rept. Inst. Freshw. Res. Drottningholm, 45: 113—189.

Appendix, fig. 38.

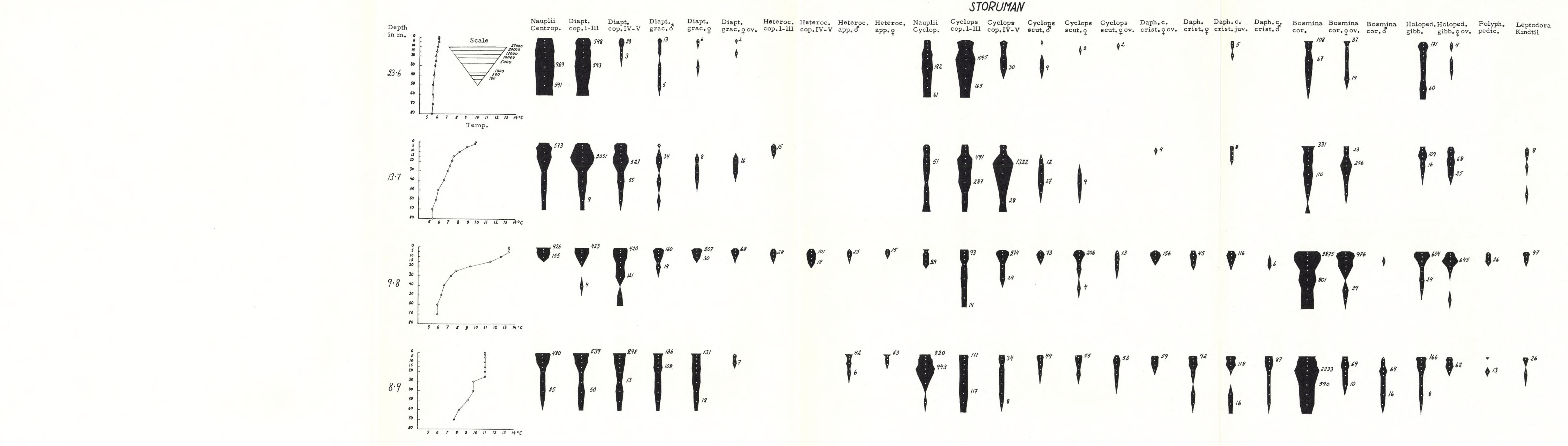


Lötmarker, Rept. Inst. Freshw. Res. Drottningholm, 45: 113—189.

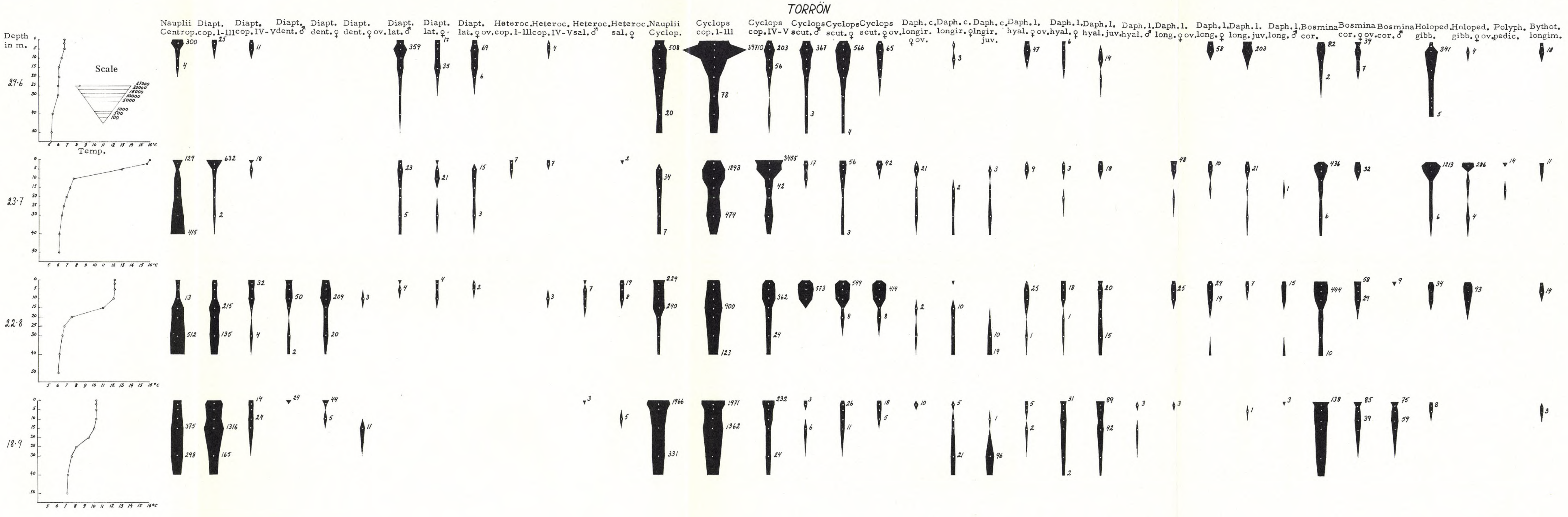
Appendix, fig. 39.



STORSJOUTEN



Lötmarker, Rept. Inst. Freshw. Res. Drottningholm, 45: 113—189.


TORRÖN
Depth in m.
Scale
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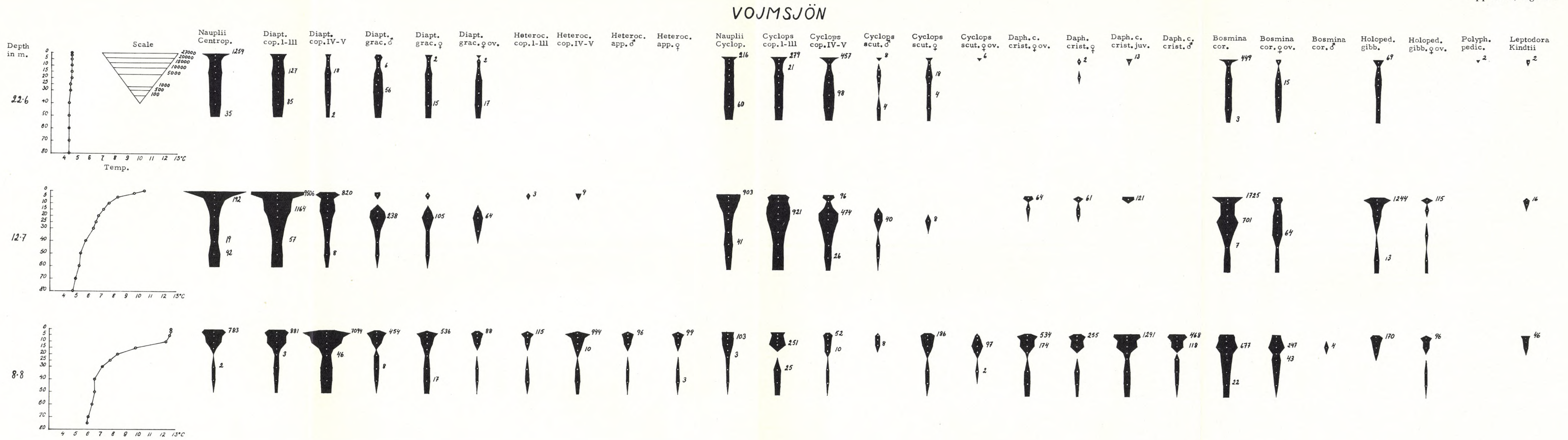
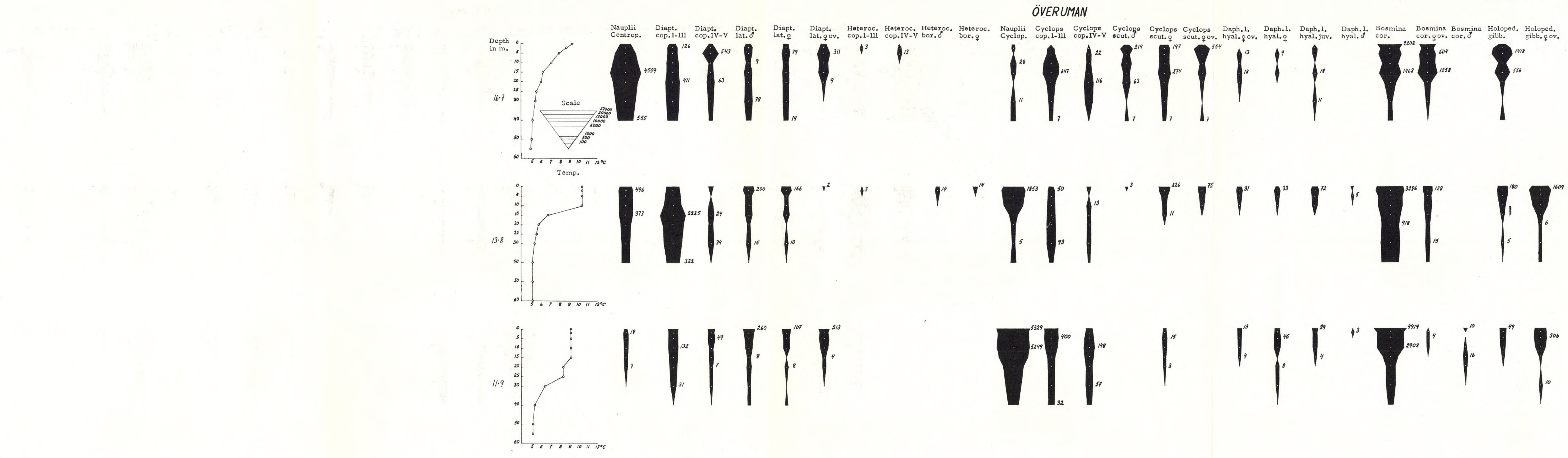
20000
15000
10000
5000
1000
500
100
Temp.
°C
29·6
23·7
22·8
18·9
Nauplii Centrop.
Diapt. cop. I-III
Diapt. cop. IV-V
Diapt. dent. ♂
Diapt. dent. ♀
Diapt. dent. ♀ ov.
Diapt. lat. ♂
Diapt. lat. ♀
Diapt. lat. ♀ ov.
Heteroc. cop. I-III
Heteroc. cop. IV-V
Heteroc. sal. ♂
Heteroc. sal. ♀
Nauplii Cyclop.
Cyclops cop. I-III
Cyclops cop. IV-V
Cyclops scut. ♂
Cyclops scut. ♀
Cyclops scut. ♀ ov.
Daph. c. longir. ♀ ov.
Daph. c. longir. ♀
Daph. c. lngir. juv.
Daph. l. hyal. ♀ ov.
Daph. l. hyal. ♀
Daph. l. hyal. juv.
Daph. l. hyal. ♂
Daph. l. long. ♀ ov.
Daph. l. long. ♀
Daph. l. long. juv.
Daph. l. long. ♂
Bosmina cor.
Bosmina cor. ♀ ov.
Bosmina cor. ♂
Holoped. gibb.
Holoped. gibb. ♀ ov.
Polyph. pedic.
Bythot. longim.

Appendix, fig. 43.





Lötmarker, Rept. Inst. Freshw. Res. Drottningholm, 45: 113—189.

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