FISHERY BOARD OF SWEDEN

INSTITUTE OF FRESHWATER RESEARCH

DROTTNINGHOLM

Report No 46

LUND 1965
CARL BLOMS BOKTRYCKERI A.-B.

FISHERY BOARD OF SWEDEN

INSTITUTE OF FRESHWATER RESEARCH

DROTTNINGHOLM

Report No 46

LUND 1965
CARL BLOMS BOKTRYCKERI A.-B.

Contents

In Memoriam

SVEN RUNNSTRÖM

4.4.1896—25.12.1964.

In the earlier part of his career Dr. Sven Runnström spent almost two decades as a marine biologist in Norway, where he made outstanding contributions to research on the influence of temperature on marine animals, e.g. the herring. In 1937 he joined the staff of the Institute of Freshwater Research.

He specialized on the consequences of the hydroelectric industry, especially the fish-population changes in lake reservoirs. His research and his submissions to the Water Courts provided a basis for a sound management of these new ecosystems.

He became the director of the Institute in 1948 and retired in 1963.

Sven Runnström's encouragement and friendship will be greatly missed by his staff members as well as by the numerous friends in all parts of the world who have acclaimed his important contributions to aquatic biology.

Papers by Prof. Dr. Sven Runnström

1. 1919. und J. RUNNSTRÖM. Über die Entwicklung von *Cucumaria frondosa* (GUNNERUS) und *Psolus phantapus* (STRUSSENFELT). *Bergens Museums Årbok 1918—19. Naturvidensk. rekke, Nr. 5, 1—99.*
2. 1922. Några nya undersökningar över förvärvade egenskapers ärftlighet. *Naturen, Oslo, 46 Årg. 133—144.*
3. 1923. Några nya försök över transplantation. (Från ett besök vid den biologiska försöksanstalten i Wien). *Naturen, Oslo, 47. Årg. 217—232.*
4. 1925. Beitrag zur Kenntnis einiger hermaphroditischen Dekapoden Crustaceen. *Bergens Museums Skrifter. Ny rekke. B. III, No. 2, 1—115.*
5. 1925. *Leptosynapta inhaerens,* en holothurie med förkortad utveckling. *Bergens Museums Årbok 1923—24. Naturvidensk. rekke, Nr. 8, 1—8.*
6. 1925. Zur Biologie und Entwicklung von *Balanus balanoides* (LINNÉ). *Bergens Museums Årbok 1924—25. Naturvidensk. rekke, Nr. 5, 1—46.*
7. 1925. Temperatur och utbredning, några experimentellt-biologiska undersökningar. *Naturen, Oslo. 49. Årg. 268—288.*
8. 1926. Über die Plattenentwicklung von *Verruca strömia* (O. F. MÜLLER). *Bergens Museums Årbok 1926. Naturvidensk. rekke, Nr. 3, 1—19.*
9. 1927. Über die Entwicklung von *Leptosynapta inhaerens* (O. F. MÜLLER). *Bergens Museums Årbok 1927. Naturvidensk. rekke, Nr. 1, 1—80.*
10. 1927. Über die Larve von *Strongylocentrotus dröbachiensis* (O. F. MÜLLER). *Nyt Mag. f. Naturv. B. 65, 307—320.*
11. 1927. *Amphipoda, Isopoda* and *Pycnogonida* from the Siberian Arctic Ocean. The Norwegian north polar expedition with the »Maud» 1918—1925, Scientific results. Vol. V. No. 8, 1—18.
12. 1928. Über die Thermopathie der Fortpflanzung und Entwicklung mariner Tiere in Beziehung zu ihrer geographischen Verbreitung. Eine experimentell ökologische Studie. *Bergens Museums Årbok 1927. Naturvidensk. rekke, Nr. 2, 1—67.*
13. 1929. Eine neue Spatangidlarve von der Westküste Norwegens. *Bergens Museums Årbok 1929. Naturvidensk. rekke, Nr. 9, 1—7.*
14. 1929. Weitere Studien über die Temperaturanpassung der Fortpflanzung und Entwicklung mariner Tiere. *Bergens Museums Årbok 1929. Naturvidensk. rekke, Nr. 10, 1—46.*
15. 1930. Sildeundersøkelsene 1928/29 og 1929/30. *Årsberetning vedk. Norges Fiskerier, 1930: 1, 1—5.*
16. 1930. Om djurlivet på fjordbottnens sand och lerslätter. *Naturen, Oslo, 54. Årg. 10—24.*
17. 1931. Sildeundersøkelser 1930—31. *Årsberetning vedk. Norges Fiskerier 1931: 1, 1—13.*
18. 1931. Vom Moorschneehuhn. *Wild und Hund, Berlin, 37. Jahrg. 868—870.*
19. 1932. Eine Uebersicht über das Zooplankton des Herdla- und Hjeltefjordes. *Bergens Museums Årbok 1931. Naturvidensk. rekke, Nr. 7, 1—67.*

20. 1932. Sildeundersøkelsene 1931—32. *Årsberetning vedk. Norges Fiskerier, 1932:1, 1—6.*
21. 1933. Über die Rassenverhältnisse bei den norwegischen Früjahrshering mit besonderer Berüchsichtigung der Konstanz der Rassenmerkmale. *J. Cons. Vol. VIII. No. 2. 235—249.*
22. 1933. Sildeundersøkelsene 1932—33. *Årsberetning vedk. Norges Fiskerier, 1933, 49—52.*
23. 1934. The Pelagic Distribution of the Herring Larvae in the Norwegian Waters. *Rapp. Cons. Explor. Mer, Vol. LXXXVIII, 3—6.*
24. 1934. Om den norske silds gyteinnsig og rase forhold. *Naturen, Oslo, 58. Årg. 129—186.*
25. 1935. The Relationship between the Spring-Spawning Herring Population of the Northern North Sea and the Norwegian West Coast. *Rapp. Cons. Explor. Mer, Vol. XCIV, 3—6.*
26. 1935. Kan vi udvide storsild- og fetsildfisket ved å søke nye fiskeplasser? *Bergens Tidende, d. 18.5, 14—15.*
27. 1936. Die Anpassung der Fortpflanzung und Entwicklung mariner Tiere an die Temperaturverhältnisse verschiedener Verbreitungsgebiete. *Bergens Museums Årbok 1936. Naturvidensk. rekke Nr 3, 1—36.*
28. 1936. A Study on the Life History and Migrations of the Norwegian Spring-Herring based on the Analysis of the Winter Rings and Summer Zones of the Scale. *Fiskeridir. Skr. Havundersøk. Vol. V, No. 2, 1—103.*
29. 1936. Investigation on Icelandic Herring in 1929—35. *Rapp. Cons. Explor. Mer, Vol. XCIX, 3—11.*
30. 1937. A Review of the Norwegian Herring Investigations in Recent Years. *J. Cons. Vol. XII, No. 2, 123—143.*
31. 1937. Sildeundersøkelsene 1936. *Årsberetning vedk. Norges Fiskerier 1936. 1—11.*
32. 1937. Bare en liten del av sildebestanden blir gjenstand for fiske. *Bergens Tidende, d. 27.2, 16—17.*
33. 1938. Sildeundersøkelsene 1937. *Årsberetning vedk. Norges Fiskerier 1937. 1—13.*
34. 1940. Vänerlaxens ålder och tillväxt. (Age and growth of the Salmon in Lake Vänern. Summary). *Rep. Inst. Freshw. Res. Drottningholm. Vol. 18, 1—39.*
35. 1940. Om trubbnosig och spetsnosig ål. *Svensk Fisk. Tidskr. Årg. 49, 161—164.*
36. 1941. Racial Analysis of the Herring in Norwegian Waters. *Fiskeridir. Skr. Havundersøk. Vol. VI, No. 7, 1—110.*
37. 1941. Quantitative Investigations on Herring Spawning and its yearly Fluctuations at the West Coast of Norway. *Fiskeridir. Skr. Havundersøk. Vol. VI, No. 8, 1—71.*
38. 1941. Vårlekande siklöja. *Svensk Fisk. Tidskr. Årg. 50, 49—53.*
39. 1944. Om smärlingen från några Jämtlandssjöar. *Svensk Fisk. Tidskr. Årg. 53, 25—29.*
40. 1946. Sjöregleringar och fisket. *Lantbruksveckan 1946, 141—163.*
41. 1948. Forskningen och fiskerinäringen. *Tiden, Stockholm, Årg. 40, 108—110.*
42. 1949. Director's Report for the Year 1948. *Rep. Inst. Freshw. Res. Drottningholm. No. 29, 5—28.*
43. 1949. Control of Trout Migration by a Fish Ladder. *Rep. Inst. Freshw. Res. Drottningholm. No. 29, 85—88.*
44. 1950. Director's Report for the Year 1949. *Rep. Inst. Freshw. Res. Drottningholm. No. 31, 5—18.*
45. and A. MÄÄR. 1950. *Lepidurus arcticus* (PALLAS) in Indalsälven and Faxälven watersystems, Sweden and Norway. *Rep. Inst. Freshw. Res. Drottningholm. No. 31, 147—150.*
46. 1950. Sillens mysterium löses? *Svensk Fisk. Tidskr. Årg. 59, 53—54.*
47. 1951. Director's Report for the Year 1950. *Rep. Inst. Freshw. Res. Drottningholm. No. 32, 5—14.*
48. 1951. The Population of Char, *Salmo alpinus,* LINNÉ, in a Regulated Lake. *Rep. Inst. Freshw. Res. Drottningholm. No 32, 66—78.*

49. 1951. En sjöreglerings inverkan på fiskbeståndet. *Svenska Vattenkraftföreningens Publikationer 422 (1951: 7), 111—131.*
50. 1952. Director's Report for the Year 1951. *Rep. Inst. Freshw. Res. Drottningholm. No. 33, 5—16.*
51. 1952. The Population of Trout, *Salmo trutta,* LINNÉ, in Regulated Lakes. *Rep. Inst. Freshw. Res. Drottningholm. No. 33, 179—198.*
52. 1952. Fiskodlingsfrågans aktuella läge. *Svensk Fisk. Tidskr. Årg. 61, 178—183.*
53. 1953. Director's Report for the Year 1952. *Rep. Inst. Freshw. Res. Drottningholm. No. 34, 5—13.*
54. 1954. Director's Report for the Year 1953. *Rep. Inst. Freshw. Res. Drottning. No. 35, 5—10.*
55. 1955. Changes in fish production in Impounded lakes. *Verh. int. Ver. Limnol. Vol. XII, 176—182.*
56. 1955. Director's Report for the Year 1954. *Rep. Inst. Freshw. Res. Drottningholm. No. 36, 5—12.*
57. och G. SVÄRDSON. 1956. Siklöjans artbildning. *Svensk Fisk. Tidskr. Årg. 65, 53—55.*
58. 1956. Publiceringen av fiskets forskningsresultat. *Svensk Fisk. Tidskr. Årg. 65, 89—90.*
59. 1957. Migration, age and growth of the brown trout (*Salmo trutta* L.) in Lake Rensjön. *Rep. Inst. Freshw. Res. Drottningholm. 38, 194—246.*
60. 1962. Professor Dr. GUNNAR ALM in memoriam. *Hydrobiologia, Vol. XX, No. 2, 202—212.*
61. 1962. Allmän överblick av den biologiska forskningen rörande sjöregleringar. *Svensk Fisk. Tidskr. Årg. 71, 1—3.*
62. 1962. Regleringens inverkan på öringens och rödingens tillväxt i sjön Ransaren. *Svensk Fisk. Tidskr. Årg. 71, 170—174.*
63. 1962. Vattenkraften och fisket. *Jakt—Fiske—Friluftsliv, Oslo, 91. Årg. 306—317.*
64. 1964. Effects of impoundment on the growth of *Salmo trutta* and *Salvelinus alpinus* in Lake Ransaren. (Swedish Lappland). *Verh. int. Ver. Limn. Vol. XV, 453—461.*
65. 1964. Kontroll av Jormsjöns lekrödingbestånd i Blåsjöälven genom en fiskspärr samt studier över dess vandringar genom märkningsförsök. *Information 1964, Nr 4.*

The short-term effect of artificial water-level fluctuations upon the littoral fauna of Lake Kultsjön, northern Sweden

By Ulf Grimås

Entomological Department
Zoological Institute, Uppsala

Contents

1. Introduction

The literature on artificial water-level fluctuations and bottom fauna contains information indicating that the short-term effect of lake regulation differs from the long-term effect with regard to the reaction of the organisms and the composition of the fauna as a whole.

The flourishing of benthic crustaceans immediately after an impoundment, established for the first time by Dahl (1926) in Norwegian lakes, has in later times been confirmed in connection with different kinds of disturbance in the water-level fluctuation of lakes (cf. Grimås 1962).

For other bottom organisms the available information is less definite.

For Lake Minnewanka Cuerrier (1954) reports a decrease in the abundance of bottom animals, a decrease which was most pronounced immediately after the interference with the lake.

In the subarctic Lake Ransaren, northern Sweden, Nilsson (1964) observed a similar sharp decrease in the abundance of the bottom animals, immediately after the interference, followed by a certain reconstruction within the fauna. After the first year of the regulation the density of individuals in the upper littoral dropped from 15,073 to 132 ind. per sq. metre, i.e. by more than 99 per cent (Nilsson, private communication).

In connection with an increased lowering of the water level during winter Hynes (1961) reports from a mesotrophic lake in England a rapid reduction of many littoral animals. These losses seem to be counterbalanced by an increased abundance of oligochaetes. The indications of a re-established insect fauna in the lake after some years were supposed to be due to periods of less extreme fluctuations in level.

The diverging results of investigations in Norwegian regulated lakes (DAHL 1926, 1931, HUITFELDT-KAAS 1935) might possibly be explained by the negative short-term effect upon the aquatic insect larvae, that as a matter of fact was observed by Dahl (cf. GRIMÅS 1964).

This paper presents some results of investigations in Lake Kultsjön in northern Sweden, carried out immediately before and after an artificially induced fluctuation of the water level in the lake. Part of the material for analysis has been most obligingly supplied by Dr. N.-A. NILSSON of the Institute of Freshwater Research, Drottningholm.

2. Description of the lake

Lake Kultsjön is situated in southern Lapland at an altitude of 540 metres above sea-level. Its length is about 30 kilometres, the greatest breadth being about 3 kilometres.

LINDGREN (1963), in his description of the lake, reports the maximum temperature of the surface water in 1958 as 12.7°C, and a thermal stratification in the lake lasting from the middle of July to the middle of September. The chemical properties of the water from the western basin of the lake during 1957—1958 confirm the oligotrophic character of the lake. The specific conductivity ($H_{20} \cdot 10^6$) varies between 24 and 45, the alkalinity (μequiv/l) between 150 and 350, calcium+magnesium (μmol/l) between 94 and 202, and the pH between 6.5 and 7.4. The values for free phosphate and nitrate (μg/l) vary between 0.0 and 1.6 and 0 and 51, respectively.

Since the winter of 1958—59 the lake has served as a water storage basin. The annual amplitude of the water level amounts to 5 vertical metres. This means that the summer water level is about 1 metre above what is normal in the lake. The draw-down phase occurs during winter and early spring (Fig. 1). The area of the regulated zone amounts to 18 sq. km, representing *c.* 30 per cent of the total area of the lake at the new highwater level.

An increased annual amplitude of the water level brings about an intensified redeposition of loose sediments derived from the area of regulation. This finds its expression in, amongst other things, a decreased transparency of the water. Fig. 2 shows that the transparency in Lake Kultsjön varied between 5.8 and 10.0 m during the years 1959 and 1960. The course of the curve appears typical for a regulated lake immediately after an interference (cf. GRIMÅS 1962). Instead of a high transparency after the breaking-up of the ice, as has been reported from neighbouring oligotrophic lakes (MÄÄR,

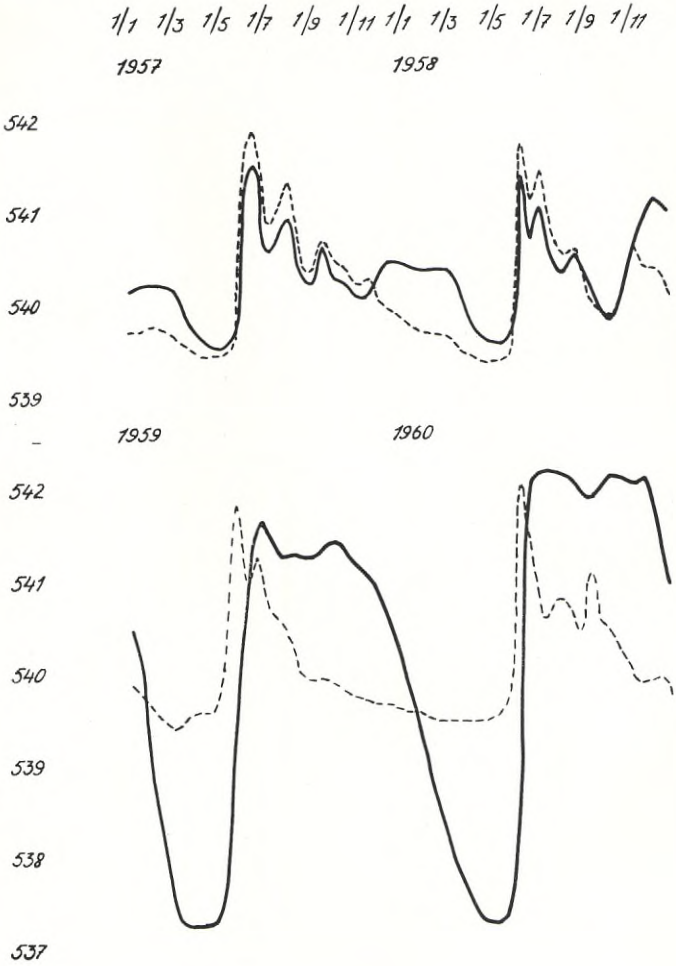


Fig. 1. Lake Kultsjön. The water-level fluctuations before and after the impoundment. Broken line: estimated natural water level.

in manuscript, BRUNDIN 1949, GRIMÅS 1961), the impounded lake exhibits a minimum in spring, followed by increasing transparency in the course of the summer.

The pattern of the curves for Lake Kultsjön during 1957—58 suggests the possibility that the water of the lake is influenced by turbidity resulting from human activities upstream of the lake even before its regulation. This influence during 1957—58 can also be recognized in Fig. 1. The difference between the actually observed and the calculated natural variations of the water level is due to the amount of water discharged from the impounded Lake Ransaren upstream, resulting, among other things, in a greater than normal supply of water to Lake Kultsjön in winter and a diminished annual amplitude.

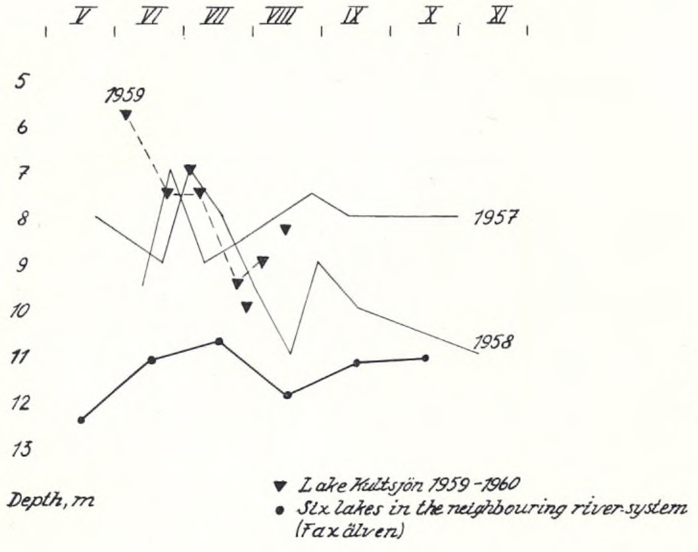


Fig. 2. Transparency in Lake Kultsjön and six neighbouring lakes.

3. Methods and Material

The quantitative material was collected by means of a bottom sampler, type Ekman-Birge, covering an area of 225 sq. centimetres. The sifting was carried out through 0.6 millimetre mesh. The preserved material was weighed to a limit of ±0.1 milligramme.

The depth zones have been calculated with reference to an approximate summer water level prior to the regulation (541 metres above see level).

Both in June 1958 and 1960 sampling was carried out at the same station, viz. "Prestnäset" in the western basin of the lake. Material for comparison is available also from the eastern part of the lake, "Saxnäs", where it was collected in January 1958. The material comprises about 4,000 animals, derived from 62 quantitative samplings of the bottom. Additional samples of the bottom were taken at "Prestnäset" in 1959 during the month of April, when the water level is at the draw-down limit and the bottoms of the regulated area are exposed and frozen.

The material does not cover the season for the maximum development of small crustaceans, e.g. benthic cladoceres, which can be reckoned to take place in August. The normal positive short-term effect upon these animals therefore finds no expression in the results, and does not influence the relative share of the other organisms in the fauna.

The material has been divided into four main groups. The first group, "fish food", comprises those elements of the fauna that are known to be of great importance as fish food in the lake (cf. Nilsson 1955, 1963), viz. *Gam-*

marus, larvae of *Ephemeroptera, Trichoptera, Plecoptera, Coleoptera* and *Gastropoda. Chironomidae* and *Oligochaeta* form two main groups of their own, while other animals are lumped together as a fourth group under the designation "remainder".

4. Results

Quantity. Table 1 gives the medium values of biomass and abundance of bottom animals in the various depth zones before and after the regulation.

The severest losses occur in the areas which have been rendered dry during the winter (zone 0—5 metres). There the loss in weight and number of bottom animals can be estimated at 89 and 86 per cent, respectively (cf. Fig. 3).

Table 1. Lake Kultsjön. The biomass and abundance of bottom animals in the littoral during the month of June before and after the impoundment.

Depth zone	Weight, g/sq. m			Number, indiv./sq. m		
	1958	1960	decrease (per cent)	1958	1960	decrease (per cent)
0—1	8.50	—	—	2,746	—	—
1—2	14.90	0.76	95	5,166	388	93
2—4	7.40	1.47	80	3,661	696	81
5—7	2.11	1.20	43	2,059	634	69
8—10	1.64	1.16	25	1,303	678	50
0—5	10.27	1.11	89	3,857	543	86
5—10	1.88	1.18	37	1,682	657	61
0—10	6.07	1.14	81	2,770	600	78

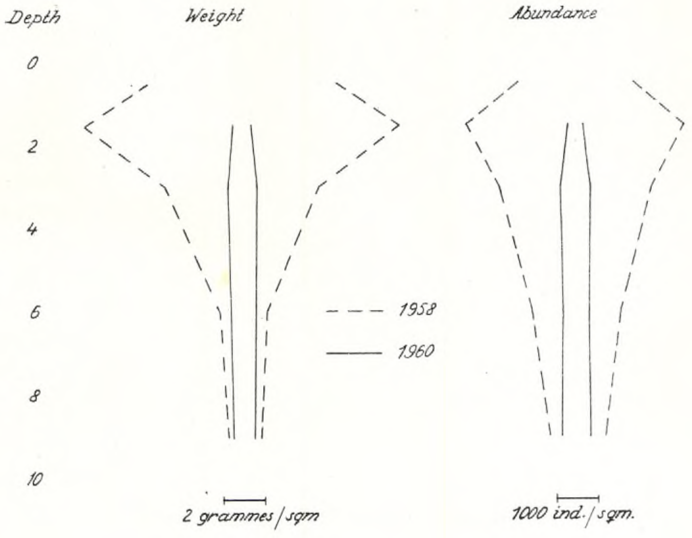


Fig. 3. Lake Kultsjön. The bathymetrical distribution of the bottom fauna before and after the impoundment.

Table 2. Lake Kultsjön. The biomass and abundance of bottom animals during January and June, 1958.

	"Fish food"	Chironomids	Oligochaetes	Remainder	Total
Weight, g/sq. m					
January, 1958	0.77	1.92	1.07	0.56	4.32
June, 1958	1.35	2.59	1.70	0.43	6.07
Number, ind./sq. m					
January, 1958	151	2,876	539	402	3,968
June, 1958	135	1,793	567	275	2,770

Great changes have taken place also within other portions of the littoral, i.e. below the drainage limit. In spite of the fact that these bottoms are not directly influenced by the draining, 60 per cent of their animals disappear, and the average weight per sq. metre drops by almost 40 per cent.

The entire littoral can thus be characterized as uniformly poor in individuals, and without any divergent depth zones with greater abundances (Fig. 3). In this respect Lake Kultsjön of 1960 differs not only from natural lakes but also from lakes which have been for a long time under the influence of regulation.

The results obtained in January 1958 from the opposite end of the lake exhibit minor deviations from the figures given for June 1958 (Table 2). The medium values for the entire littoral indicate a small number of individuals but a greater medium weight of bottom animals per sq. metre during June. This can be due to differences in environment and fauna between the two regions in the lake, but can also be interpreted as the combined effect of predation and individual growth during the spring months. The larvae of insects, especially, show a reduced abundance, but an increase in weight in the material from the winter to the spring.

Quality. The situation before the regulation is evident from Tables 3, 4 and 5. Fig. 4 shows also the composition of the fauna in the eastern end of the lake in January 1958.

The results obtained in 1958 at the two stations in the lake agree on the whole with regard to the balance between the four chosen main groups within the fauna. There is a high relative abundance of the chironomids, which for the entire littoral can be estimated at more than 65 per cent. This great wealth of individuals can be connected with the season, and is probably typical for natural lakes within the area. A large proportion of the material from June are pupae and the emergence does not seem to have begun in the littoral. In comparable sub-arctic lakes in the Swedish high mountains most of the chironomids leave the bottom in the course of July and August

Table 3. Lake Kultsjön. The relative abundance of bottom animals in the depth zone 1—10 metres before and after the impoundment.

	1958 %	1960 %
Chironomidae	65.6	16.9
Large insect larvae	2.0	0.4
Gammarus lacustris	2.8	—
Gastropoda	0.7	—
Nematoda	1.3	—
Hirudinaea	1.0	—
Copepoda	0.1	—
Oligochaeta	21.9	66.2
Pisidae	4.2	11.7
Hydracarina	0.1	2.6
Diptera [excl. *Chir.*]	0.3	2.2

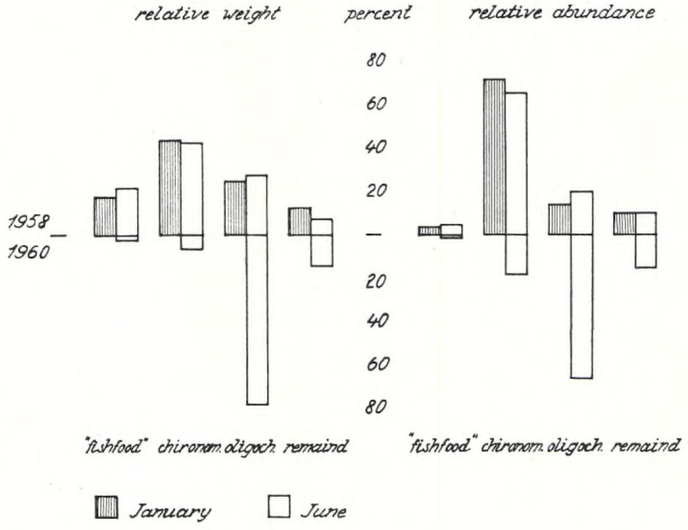


Fig. 4. Lake Kultsjön. The qualitative composition of the bottom fauna before and after the impoundment.

(Thienemann 1942, Brundin 1949), and the emergence in the early spring seems to be restricted mainly to the region of the profundal (cf. Grimås 1961). A great abundance of larvae in June has likewise been found in the neighbouring, unregulated Lake Ankarvattnet (Grimås 1961).

The dominance of the chironomids is less pronounced as regards the weight. In the upper littoral the substantial "fish food" organisms play a considerable rôle, and towards the deeper littoral oligochaetes take over the dominant position. Most important among the other organisms are the pisidians, the absolute and relative abundance of which decreases within the middle parts of the littoral, with their rich vegetation.

Since the regulation, in 1960, the balance between the four main groups of the bottom fauna has changed. Now the littoral fauna of Lake Kultsjön

Table 4. Lake Kultsjön. The biomass of the four main groups of bottom animals before and after the impoundment. In grammes per sq. metre.

Depth zone	"Fish food" 1958	"Fish food" 1960	Chironomids 1958	Chironomids 1960	Oligochaetes 1958	Oligochaetes 1960	Remainder 1958	Remainder 1960
0—1	2.53	—	4.72	—	0.62	—	0.63	—
1—2	3.24	0.08	5.90	0.05	4.99	0.59	0.77	0.04
2—4	2.07	—	3.35	0.02	1.85	1.43	0.13	0.02
5—7	0.18	—	0.85	0.11	0.94	1.05	0.14	0.04
8—10	—	—	0.22	0.11	0.88	0.49	0.54	0.56
0—5	2.61	0.03	4.66	0.04	2.49	1.01	0.51	0.03
5—10	0.09	—	0.54	0.11	0.91	0.77	0.34	0.30
0—10	1.35	0.02	2.59	0.07	1.70	0.89	0.43	0.16

Table 5. Lake Kultsjön. The abundance of the four main groups of bottom animals before and after the impoundment. Individuals per sq. metre.

Depth zone	"Fish food" 1958	"Fish food" 1960	Chironomids 1958	Chironomids 1960	Oligochaetes 1958	Oligochaetes 1960	Remainder 1958	Remainder 1960
0—1	88	—	1,945	—	229	—	484	—
1—2	431	9	3,670	62	942	264	123	53
2—4	238	—	2,675	53	722	625	26	18
5—7	35	—	1,276	150	572	466	176	18
8—10	—	—	370	141	431	229	502	308
0—5	252	4	2,763	58	631	445	211	36
5—10	18	—	823	146	502	348	339	163
0—10	135	2	1,793	102	567	397	275	99

can be characterized as a pronounced oligochaet fauna (Table 3, Fig. 4).

In practically all depth zones all groups of animals have decreased both in abundance and weight. The typical "fish food" organisms are almost completely eliminated from the entire littoral. Of the chironomid fauna only a small remainder is left below the draw-down limit. The oligochaets are comparatively little influenced (Table 6) and therefore occupy a dominant position. Of the other organisms, hydracarines, some tipulids, empidids and, in the deepest parts of the littoral, pisidians are left.

The organisms which before the regulation were most important as fish food are *Gammarus lacustris* SARS with a maximum abundance in the depth zone 1—2 metres in June, the gastropods *Gyraulus acronicus* FER. and *Lymnæa peregra* MÜLL., and the ephemerid *Chitonophora mucronata* BENGTS. The material of 1958 contains 11 additional species of large insects, viz. the ephemerids *Siphlonurus lacustris* ETN. and *Centroptilum luteolum* MÜLL., the trichopters *Phryganea obsoleta* MCLACHL., *Phr. grandis* L., *Agraylea cognatella* MCLACHL., *Mystacides azurea* L., *Limnophilus* sp., *Molanna* sp., and *Halesus* sp., the plecopter *Nemoura* sp., and the coleopter *Haliplus fulvus* FABR. In June 1958 all these fish-food organisms with the exception of

Table 6. Lake Kultsjön. The percentage decrease of littoral animals as a short-term effect of impoundment.

Depth zone, metres	"Fish food"	Chironomids	Oligochaetes	Remainder	Total
Percentage decrease in weight					
0—5	99	99	59	94	89
5—10	100	79	15	13	37
0—10	99	97	48	62	81
Percentage decrease in number					
0—5	98	98	30	83	86
5—10	100	82	31	52	61
0—10	99	94	30	64	78

Table 7. Lake Kultsjön. The abundance of chironomid larvae in the littoral before and after the impoundment.

Depth zone	*Tanypodinae*	*Orthocladiinae*	*Chironomini*	*Tanytarsini*	Total
1958, June					
0—5	569	393	1,317	484	2,763
5—10	352	370	44	57	823
0—10 (per cent)	24	19	41	16	—
1960, June					
0—5	13	5	31	9	58
5—10	9	102	22	13	146
0—10 (per cent)	11	53	25	11	—

Phryganea obsoleta are limited to the upper half of the littoral. In the material collected in January of the same year their distribution seems to extend towards deeper regions. An example is *Gammarus lacustris,* which then occurred in the entire littoral from 0 to 10 metres with a maximum abundance in the zone 5—7 metres.

Of these fish-food organisms only *Haliplus fulvus* has been encountered in the littoral of the lake after the regulation.

The composition of the chironomid fauna of the littoral is altered by the regulation (Table 7).

Among the material of June 1958 40 per cent belong to the main group *Chironomini.* As in many sub-arctic and arctic lakes *Stichtochironomus rosenschöldi* EDW. (cf. LENZ 1928, BRUNDIN 1949) is abundant in the upper and middle littoral. Among other we can mention *Chironomus anthracinus* ZETT., *Polypedilum,* and *Cryptochironomus. Tanytarsini* as well as *Chironomini* are represented by the greatest number of individuals in the upper littoral, most of them belonging to the genera *Tanytarsus* and *Paratanytarsus.*

Table 8. Lake Kultsjön. The biomass and abundance of bottom animals during the draw-down period [April 1959].

	"Fish food"	Chironomids	Oligochaetes	Remainder	Total
Frozen in bottom (0—2 m)					
weight g/m² ..	0.03	0.74	2.64	2.47	5.88
number ind./m²	75	2,488	791	845	4,199
Below draw-down limit (5—7 m)					
weight	0.27	3.16	1.62	0.38	5.43
number	205	3,681	1.188	440	5,514

Orthocladiinae and *Tanypodinae* are uniformly distributed throughout the entire littoral.

From the period since the regulation only a small material is available. If the littoral is taken as a unit, however, it seems as if the relative share of the *Orthocladiinae* had increased as a short-term effect while the regulation first of all causes a reduction of the forms living in the upper littoral.

Like the *Oligochaeta* some other groups of animals exhibit an increased abundance after the regulation.

The *Pisidae,* which in January and June, 1958 formed 5 per cent of the fauna, account after the regulation for 12 per cent. This increase can be attributed to their occurrence in the deeper parts of the littoral.

A minor increase can be noted also for *Hydracarina* and larvae of *Empididae* and *Tipulidae,* viz. from < 1 per cent to 3 and 2 per cent, respectively.

Among the animals within the main group "remainder" that have not been rediscovered since the regulation we can mention the hirudinean *Helobdella stagnalis* L.

The winter situation. In April 1959 samples of the bottom fauna were taken both within the depth zone of 0—2 metres and immediately below the draw-down limit (Table 8).

In the frozen bottoms three vertical layers can be distinguished, viz. lake ice containing frozen water plants, the frozen surface layer of the sediments, and non-frozen soft bottom sediments.

A comparison between these three zones reveals a vertical zoning of the animal groups. In the vegetation layer insects, especially chironomids, are strongly dominant, but during summer the fauna is probably richer in periphytic forms, e.g. minor crustaceans. The uppermost frozen surface layer of the sediment contains the greatest number of forms, insects and pisids being the most important. The fauna of the deeper sediments is dominated by oligochaetes.

The greatest number of dead animals, viz. 33 per cent, was encountered in the frozen aquatic vegetation (GRIMÅS 1961). In the sediments the mortality can be calculated at 11—14 per cent. The results indicate further a difference in the percentage of mortality between the different groups of animals, e.g. 100 per cent for "fish food" organisms, 40 for hirudineans, 25 for chironomids, 5 for pisidians, and 0 per cent for oligochaetes.

The total density of individuals in the frozen bottoms of the depth zone 0—5 metres has been estimated at 4,200 ind./sq. m. In comparison with the figures obtained for June 1958 this value appears normal for the depth zone. The balance between the different animal groups exhibits no essential changes. Of the total number of animals the larvae of chironomids account for 60 per cent, while the oligochaetes form 19 per cent.

The weight of the fauna exhibits greater deviations from the values for the year 1958. The calculated total weight is about 6 grammes/sq. m, against about 12 grammes for 1958. This low value is partly due to the fact that the larvae of many insects are in an early phase of development, and that the dead organisms weigh much less than the living ones. Also an emigration of larger, more mobile animals might contribute to the result.

Immediately below the draw-down limit (calculated depth zone 6 metres) both the number of individuals and the biomasse have increased for all groups of animals in the fauna. Of the total number of animals the chironomids account for 67 per cent, the oligochaetes for 22 per cent. The balance within the *Chironomidae* appears to be unchanged, *Orthocladiinae* and *Tanypodinae* being the most important elements; this seems normal, having regard to the depth.

5. Discussion

The bottom fauna of Lake Kultsjön existing immediately after the regulation differs in several respects from that of older regulated lakes with a similar annual amplitude of the water level.

From the *quantitative* point of view conditions in older regulated lakes immediately below the draw-down limit agree with those in the natural lake. Above the draw-down limit, the bathymetric distribution of the animals is inverted compared with normal conditions and towards greater depths the differences increase again (GRIMÅS 1961). Immediately after the interference the littoral of Lake Kultsjön had no depth zone with a superior density of individuals, and the sharp decrease in abundance likewise comprises littoral areas that are not under the direct influence of the regulation. The comparison with the older regulated lakes might therefore suggest that the great quantitative losses express a short-term effect of the regulation, and that a regeneration of the bottom fauna might be expected occur first of all in regions below the drainage area.

Also the *qualitative* composition of the bottom fauna seems to be under the influence of a pronounced short-term effect. On account of the season for the investigation no flourishing of benthic cladocers could be definitely established, but it can be traced in a changed food choice of the fish fauna of the lake (NILSSON, private communication). The changes in the balance between the other organisms of the bottom fauna differ from those known from older regulated lakes. An increasing age of regulation normally seems to bring about an increased relative abundance of the chironomids, as has been noticed in many lakes (CUERRIER 1954, RAWSON 1958, MILLER and PAETZ 1959, GRIMÅS 1961, 1964, AASS 1963). The littoral fauna of Lake Kultsjön in spring, which originally could be characterized as a chironomid fauna, has, however, been changed by the regulation into an oligochaete fauna.

In some instances the aspects of the bottom fauna in Lake Kultsjön agree with the conditions in older regulated lakes. After the short period of regulation many major insects, crustaceans, and gastropods are entirely missing, while on the other hand organisms like pisidians, hydracarines, empidids, and tipulids show a tendency towards taking a greater relative share in the total fauna.

The explanation of the characteristic course of development immediately after an interference has to be sought in passing disturbances of the environment. A later phase brings about a stabilization of the environment and a new settlement of species that fit the new conditions in the lake.

Simultaneously with a reduction of the bottom vegetation a slow improverishment in organogenic material starts, especially in the sediments of the littoral. Thus during the first year of impoundment there is a relatively good supply of food for organisms feeding on detritus, e.g. oligochaetes, while the supply of living vegetable matter is considerably reduced (cf. QUENNERSTEDT 1958). This has an immediate effect upon such herbivores as are dependent upon fresh vegetable substances. An equally fast and direct selective effect upon the fauna may be exerted by the drying-up and the refrigeration during the first winter. These extreme conditions are, however, annually recurrent and do not explain the typical shock-like, short-term effect upon the total fauna in the entire littoral.

The results from Lake Kultsjön suggest that the immediately induced structural changes in the environment constitute an important factor within the short-term effect. As an example can be mentioned the unstable conditions in the sediments of the bottoms, resulting from an increased erosion within the zone of regulation. With the gradual removal of loose sediments from this zone conditions become stabilized. For this reason the passing effect of the regulation becomes most pronounced within the depths which are not every year directly affected by the lowering of the water, but which during the process of redeposition have received the eroded material. To judge from the situation in older regulated lakes it is in these regions below the draw-down limit that we can expect the quantitatively most important regeneration of the fauna.

Also the changes in the qualitative composition of the littoral fauna indicates the importance of the unstable environment. The varying degree of reduction can be interpreted as due to the varying dependence of the animals upon the contact layers between bottom and water. In this respect the vertical distribution in the sediments may be indicative of this dependence. In the course of the lowering of the water level of Lake Kultsjön in the first winter (April 1959) this vertical zoning of the fauna in the frozen bottom was observed.

By means of the changes in spring of the littoral fauna of Lake Kultsjön from an insect fauna to an oligochaete fauna it seems possible to make a correlation between the degree of reduction and the position or exposure of the animals in the littoral bottoms. The most profound and the fastest structural changes in the environment affect the layer of the vegetation and the surface of the sediment, the fauna of which exhibits the highest degree of reduction. This applies both within the zone of regulation and in other parts of the littoral. The only exception is provided by the limiting region towards the profundal of Lake Kultsjön, where the occurrence of pisidians indicates a restricted effect of the interference.

The initial effect of the regulation upon the fish food organisms is of especial interest. Of the 12 insects of fair size, two species of gastropods and one amphipod, which had been noted before the regulation, only 1 insect species was found again after the interference. The results indicate that in relation to other animal groups these organisms are the most severely affected. On account of their size and mobility, their exposed life upon the sediments or in the vegetation, and their normal limitation to the upper half of the littoral, they are probably particularly sensitive to the disturbances caused in the bottoms during the first years of regulation. The availability and the degree of utilization of these animals as fish food can be taken as an expression of this exposed position in the bottoms. In older regulated lakes with more stabilized conditions some major species of insects occupy areas of the bottom with fairly good supply of organogenic material within the drainage area also (GRIMÅS 1961, 1962, 1964).

The minor benthic crustaceans, especially the cladocers, react upon the short-term effect of the regulation in a way that differs from that of other bottom animals as they exhibit an actual increase in abundance. This may be due in part to a nectonic way of life in zones near the bottom surface, a circumstance which makes them less dependent upon a stable surface of sediment than are other bottom animals. The fact that they hibernate during the draining of the winter may also be of importance. The positive effect of unusually long periods of low temperatures upon the development of cladoceran populations has been estimated (DAHL 1931, ELGMORK 1964). An increased availability of food is, however, an important condition for the flourishing. The above-outlined sequence during the first year of impoundment comprises an increased flow of energy through certain channels in the ecosystem of the lake. In the neighbouring Lake Ransaren RODHE (1964) established an increased production of planktonic algae as a short-term effect, and AXELSSON (1961) found a parallel increase in the standing crop of planktonic crustaceans in the lake. In a similar way in the benthos the increased exposition of sediment probably implies an increased availability of a special type of food in layers near the bottom, the increased supply consisting either directly of particles of detritus from the sediment or indirectly of an increased bacterial flora. Under normal, unregulated conditions this type of food forms an important source of nutrition for herbivorous planktonic crustaceans (NAUWERCK 1963) and can be assumed also to be important for the development of the cladocer fauna in layers near the bottom.

One of the possibilities for the survival of littoral animals in a regulated lake is a migration towards deeper portions of the lake during the low water of winter.

The phenomenon of migration activities of bottom-living animals has been recorded by several authors (PAULY 1918, LANG 1931, BERG 1938, MUNDIE 1959). The relation between the environmental conditions and the migration is not, however, fully understood. A change within the environment, for instance a falling temperature, might cause an undirected, but increased activity of certain bottom organisms (supported by preliminary experiments in aquaria) and this in turn might facilitate a passive transport towards new areas of the bottom. Such a semi-passive drifting migration of *Chironomus*-larvae has been suggested by BARTHELMES (1963).

The results of the investigations in Lake Kultsjön during the draw-down phase do not indicate the occurrence of an extensive emigration or passive removal of the fauna of the regulation zone. The density of individuals in the frozen bottoms is high, and many species have not left their ordinary habitat in the bottoms (cf. GRIMÅS 1961). The greatest divergence is suggested within the main group of "fish food" organisms. Only gastropods and larvae of ephemerids have been encountered in the frozen bottoms. It is thus possible that in connection with the drop of temperature in autumn more mobile animals, e.g. *Gammarus,* have migrated towards deeper parts of the littoral. Such a shifting of the population of *Gammarus* was indicated as a normal phenomenon in the lake during winter.

In spite of a high abundance in the regulated zone in winter, an enrichment of all groups of animals takes place in the region immediately below the draw-down limit, where in April 1959 the concentration of bottom animals was almost three times as great as in June 1958. This enrichment was accompanied by a minute change in the balance between the different groups of animals within the depth zone, to the advantage of chironomids and fish-food organisms. This tendency towards a correlation between the activity and migration rate of the animals does not contradict the theory of a semi-passive drifting migration for the greater part of the fauna. The rapid drop of the water level and the relatively high temperature in the sediments immediately before the drying-up probably contribute to a restricted active migration in the regulated lake (cf. GRIMÅS 1961), and the enrichment below the drainage area can be considered as the result of a limited thinning-out of the fauna from a few metres above the draw-down limit. For the majority of the bottom organisms that live in the sediment, the passive removal in connection with the redeposition of the sediments during a period without ice ought to be of greater importance.

In other respects the configuration of the bottom fauna is influenced by the phenomenon of migration, induced by impoundment. It can be assumed that the greater part of the fish fauna in the lake evacuates the regulated area during the draw-down of the water. During that period about 30 per cent of the lake bottom is laid dry; this means a great reduction of the feeding ground for the fishes, without any appreciable change in the size of the fish populations.

Studies of the nutritive behaviour of fishes during winter show a continuous feeding in spite of low temperatures (cf. ZIEMIANKOWSKI and CRISTEA 1961). The feeding activity of the fishes in Kultsjön, mainly brown trout (*Salmo trutta* L.), char (*Salvelinus alpinus* L.), and burbot (*Lota lota* L.) during winter is not known. It seems possible, however, that the increased concentration of individuals during the draw-down period might increase their activity as a whole. At all events their feeding activity ought to increase during the spring (April and May), when the water level still remains at the draw-down limit.

A high concentration of predators might thus contribute to the reduction of bottom animals even below the draw-down limit and to the absence of depth zones with high abundance, when the lake is refilled in spring. The fish predation might also contribute to the fast elimination of such "fish food" organisms in the lake as can be assumed to migrate to deeper littoral regions during the draw-down period.

6. Summary

1. The short-term effect of impoundment upon the littoral fauna has been studied in the subarctic, oligotrophic Lake Kultsjön, northern Sweden.
2. The composition of the bottom fauna immediately after the impoundment differs from that of older, regulated lakes both quantitatively and qualitatively.
3. No depth zones with divergent and higher abundance of animals are found within the littoral, owing to a heavy reduction of bottom animals which even extends to littoral areas not directly influenced by draining and freezing (Fig. 3).
4. There is an altered balance of species conditioned by the impoundment. Above all there is a negative effect upon the "fish food" organisms and most insect larvae. Thereby the littoral fauna, which originally could be characterized as a chironomid fauna, has changed into an oligochaet fauna (Fig. 4).
5. Among the factors discussed, structural changes in the bottom surface are considered to be of great importance within the short-term effect.

7. References

AASS, P., 1963. Limingenreguleringens virkninger på fisket. In Norwegian, mimeographed.

AXELSSON, J., 1961. Zooplankton and impoundment of two lakes in northern Sweden [Ransaren and Kultsjön]. — *Rep. Inst. Freshw. Res. Drottning., 42,* 84—168.

BARTHELMES, D., 1963. Über die horizontale Wanderung der Teichbodenfauna. — *Z. Fisch., Bd XI N.F., Heft 3/4,* 183—187.

BERG, K., 1938. Studies on the bottom animals of Esrom lake. — *K. Danske Vidensk. Selsk. Naturv. Math. Avd., 9,* 1—255.

BRUNDIN, L., 1949. Chironomiden und andere Bodentiere der Südschwedischen Urgebirgsseen. — *Rep. Inst. Freshw. Res. Drottning., 30,* 1—914.

CUERRIER, J. P., 1954. The history of Lake Minnewanka with reference to the reaction of Lake Trout to artificial changes in environment. — *Canad. Fish. Culturist, no. 15,* 1—9.

DAHL, K., 1926. Undersökningar vid Tunnhövdfjorden angående fiskens näringsförhållanden före och efter regleringen. — *Svenska Vattenkr. Fören. Publ., 185,* 1—19. In Swedish.

— 1931. Influence of water storage on food condition of trout in Lake Paalsbufjord. — *Det Norske Vidensk.-Akad. Oslo, I, Mat.-naturv. Kl. 1: 4,* 1—53.

ELGMORK, K., 1964. Dynamics of zooplankton communities in some small inundated ponds. — *Folia limnol. scand. 12,* 1—83.

GRIMÅS, U., 1961. The bottom fauna of natural and impounded lakes in Northern Sweden [Ankarvattnet and Blåsjön]. — *Rep. Inst. Freshw. Res. Drottning., 42,* 183—237.

— 1962. The effect of increased water level fluctuation upon the bottom fauna in Lake Blåsjön, Northern Sweden. — *Rep. Inst. Freshw. Res. Drottning., 44,* 14—41.

— 1964. Studies on the bottom fauna of impounded lakes in Southern Norway. — *Rep. Inst. Freshw. Res. Drottning., 45,* 94—104.

— and NILSSON, N. A., 1962. Nahrungsfauna und Kanadische Seeforelle in Berner Gebirgsseen. — *Schweiz. Z. Hydrol. XXIV,* 49—75.

HUITFELDT-KAAS, H., 1935. Der Einfluss der Gewässregelungen auf den Fischbestand in Binnenseen. — Oslo, 1—105.

HYNES, H. B. N., 1961. The effect of water-level fluctuation on littoral fauna. — *Verh. Internat. Verein. Limnol., XIV,* 652—656.

LANG, K., 1931. Faunistisch-ökologische Untersuchungen in einigen seichten oligotrophen bzw. dystrophen Seen in Südschweden. — *Acta Univ. lund. N.F. Avd. 2 Bd. 27 Nr 18.* 1—177.

LENZ, F., 1928. Chironomiden aus Norwegischen Hochgebirgsseen. Zugleich ein Beitrag zur Seentypenfrage. — *Medd. Zool. Mus. Oslo, 12,* 111—197.

LINDGREN, Ö., 1963. Vattenbeskaffenhet och plankton i Ransaren och Kultsjön. I. Fysikalisk-kemiska förhållanden. — *Rapport fr. Limnol. inst., Uppsala,* mimeographed. In Swedish.

MILLER, R. B. and PAETZ, M. J., 1959. The effect of power irrigation and stock water developments on the fisheries of the South Saskatchewan River. — *Canad. Fish Culturist 25,* 1—44.

MUNDIE, J. H., 1959. The diurnal activity of the larger invertebrates at the surface of Lac La Ronge, Saskatchewan. — *Canad. J. Zool., Vol. 37,* 945—956.

NAUWERCK, A., 1963. Die Beziehungen zwischen Zooplankton und Phytoplankton im See Erken. — *Symb. bot. upsaliens. XVII: 5,* 1—163.

NILSSON, N.-A., 1955. Studies on the feeding habits of trout and char in north-swedish lakes. — *Rep. Inst. Freshw. Res. Drottning., 36,* 163—225.

— 1962. See GRIMÅS.

— 1963. Interaction between trout and char in Scandinavia. — *Trans. Amer. Fish. Soc., Vol. 92, No. 3,* 276—285.

— 1964. Effects of impoundments on the feeding habits of brown trout and char in Lake Ransaren [Swedish Lappland]. — *Verh. Internat. Verein. Limnol. XV,* 444—452.

PAULY, M., 1918. Zur Frühjahrswanderung der Uferfauna im grossen Müggelsee. — *Z. Fisch., Bd. 3 NF,* 77—212.

QUENNERSTEDT, N., 1958. Effect of water-level fluctuation on lake vegetation. — *Verh. Internat. Verein. Limnol., XIII,* 901—906.

RAWSON, D. S., 1958. Indices to lake productivity and their significance in predicting conditions in reservoirs and lakes with disturbed water levels. — The investigation of fish-power problems, *University of British Columbia,* 27—42.

RODHE, W., 1964. Effects of impoundment on water chemistry and plankton in Lake Ransaren [Swedish Lappland]. — *Verh. Internat. Verein. Limnol., XV,* 437—443.

THIENEMANN, A., 1942. Lappländische Chironomiden und ihre Wohngewässer. — *Arch. Hydrobiol., Suppl. Bd. XVII,* 1—253.

ZIEMIANKOWSKI, W. B. and CRISTEA, E., 1961. Beobachtungen zur Ernährungsdynamik der Fische während des Winters. — *Z. Fisch., Bd. X N.F., Heft 4/5,* 275—298.

Inlet impoundments. An attempt to preserve littoral animals in regulated subarctic lakes

By Ulf Grimås

Institute of Zoology, Entomological Department, Uppsala

Contents

1. Introduction

The bottom fauna constitutes an important intermediate link in the energy flow between plants and fish in a lake, and a rich bottom fauna is often combined with a good production of fish. Investigations have shown that the regulation of the Swedish high mountain lakes has caused a reduction of bottom animals, e.g. typical fish-food organisms of the littoral (Grimås 1961), and the reduced access to fish food finds its expression in the growth and condition of the fish (Runnström 1951, 1955, Nilsson 1961).

In recent years a number of experiments aimed at obtaining better conditions of fish production in these lakes have been constituted in Sweden. These experiments aim to preserve or restore the natural conditions of the water or to replace the destroyed natural food chains by new ones.

The significance of the regional climate for the capacity of the production is obvious in the regulated lakes. In Lake Edersee, situated in the upper part of the River Weser, Germany, the artificial water level fluctuation (32 vertical metres) is inverted, compared with that of the Swedish high mountain lakes, viz. in Edertalsperre the period of high water occurs in winter and the draw down period in summer. During a visit by the author at the end of August, 1960, the dried area was covered by a close carpet of vegetation, dominated by *Polygonum amphibium,* but also containing, i.e. *Potentilla anserina* and species of *Carex*. This vegetation ought to constitute an important component in the primary production, be an important source of food for the invading bottom organisms during the winter and finally affect the production of fish.

In Edertalsperre and in many other water reservoirs in central Europe, (cf. THIENEMANN 1911), the yield of fish is, in fact, high (MÜLLER, personal communication).

In the Swedish impounded lakes the water level must be lowered during the winter half-year in order to equalize the natural pulsation of the water in the northern river systems. This causes *inter alia,* a destruction of the bottom vegetation within the drainage zone of the lake; this means a loss of an important source of food, especially for littoral animals. The regulation has thus a negative long-term effect upon the primary production of the lake. During an early phase in the history of regulation of the lake, part of this loss is compensated by an increased flow of energy through the planktonic community of the lake (RHODE 1964). It is, however, probable that this positive effect disappears parallel with the erosion and the impoverishment of the sediments of the regulated zone (cf. LÖTMARKER 1964).

In order to obviate the worsened conditions for the fauna in the regulated zone, which often comprises the entire littoral, experiments with new food chains have been directed towards the open water and the profundal of the lakes. Many crustaceans, among them glacial relict forms, have been considered suitable new fish food organisms and *Mysis relicta* LOV., *Pallasea quadrispinosa* SARS, and *Gammaracanthus lacustris* SARS have been introduced (FÜRST 1964). The work in progress also comprises experiments with new species of fish or with hybrids which can efficiently utilize the remaining resources in the form of surface food, plankton, and fauna of the profundal, or which can be assumed to be better suited to the new biological systems. This experimental activity comprises amongst others *Salmo gairdneri* RICH. (rainbow trout), *Oncorhynchus nerka* WALB. (kokanee), *Salvelinus namaycush* WALB. (lake trout), and hybrids with *Salvelinus alpinus* L. (char) (NILSSON and SVÄRDSON 1962, EIFAC 1964).

With regard to the importance of the littoral as a feeding ground for many of our indigenous fishes, e.g. brown trout (*Salmo trutta* L.), it must be regarded as extremely valuable if in a regulated lake measures can be taken that will preserve suitable food organisms in the littoral of the lakes also.

Investigations show that the remnants of the original terrestrial vegetation, e.g. tree stumps, can serve as a food environment for many littoral organisms, which also means the preservation in the lake of typical fish-food organisms (GRIMÅS 1964).

Experience furthermore shows that the morphometric figuration of the littoral influences the productive capacity of the regulated lake. Natural disconnected areas of the regulated zone preserve a bottom fauna that in many respects resembles the original one (GRIMÅS 1962). Similar phenomena have been established by AASS (1963) in the high mountain lake Limingen in Norway. The condition can be ascribed mainly to the limited amplitude of the water level in these peripheric, disconnected ponds and the supply by the latter of organogenic material, when the erosion of the sediments of the bottoms becomes subdued.

The food available to the fish within these restricted areas does not of course, counterbalance that of the original littoral, owing amongst other things to the fact that their bottoms are accessible as feeding grounds during part of the year only. The ponds might, however, contribute to the formation of the fish fauna of the lake by favouring growth and thereby also the transition to a fish diet in a limited number of rapacious fishes, e.g. brown trout.

Against the background of the above, artificial inlet impoundments with a constant water level have been constructed in connection with the regulated subarctic lake Kultsjön, Swedish Lapland.

2. Description of the lake and the inlet impoundments

Lake Kultsjön, which is situated in southern Lapland at an altitude of 540 metres above sea level, is about 30 kilometres long and 3 kilometres broad, and can be characterized as an oligotrophic lake. A physicochemical description of the water is available in mimeographed reports from the Limnological Institute, Uppsala (LINDGREN 1963), and data have been given by RODHE (1964) and GRIMÅS (1965).

The inlet impoundments of the lake comprise two areas, viz. in connection with the feeder Saxån at the western end of the lake and with Stasån in the eastern part. They cover the original flat delta regions with disconnected tarns, formed by the feeders, which were annually inundated by the spring flood. The original vegetation was dominated by species of *Carex* and likewise contained e.g. *Caltha palustris, Viola palustris* and *V. biflora, Rubus arcticus, Pedicularis palustris, Bartsia alpina* and *Filipendula ulmaria,* together with shrubs of *Salix glauca* and *S. hastata* (NILSSON, private communication). Before the damming-up the shrubs of *Salix* and *Betula* were completely removed.

The dams were constructed in 1959. Their area totals 2.9 sq. kilometres corresponding to about 17 per cent of the area which is rendered dry by the annual fluctuation of the water-level (0—5 metres). Apart from some weeks in spring the amount of water passing through the ponds is limited (Table 1). Thus the organic drift can be assumed to be of limited importance except in the immediate vicinity of the inlet. The maximum depth occurs in the old river channel and does not exceed 5 metres. The major part of the bottoms is covered with aquatic vegetation. The sediments are mainly organogenic. The vegetation of the shallow bottoms is dominated by mosses, e.g. *Drepanocladus exannulatus, Calliergon cordifolium* and *Mnium cinclidioides* (examined by Dr SVEN NILSSON, Uppsala). *Elodoea canadensis* and

Table 1. Some data on the water supply of the inlet impoundments.

	Satsån	Saxån
Area, km^2	1.15	1.73
Area of precipitation, km^2	147	264
Drainage in days per year,		
1 litre/sec. km^2	363	—
5 ,,	229	—
10 ,,	170	—
15 ,,	137	—
20 ,,	112	—
25 ,,	94	—
50 ,,	50	—
100 ,,	19	—
Maximum high-water flow, m^3/sec.	80	190
Normal high-water flow, m^3/sec.	34	80 (spring flood)
Normal flow, m^3/sec.	3.5	8.5
Normal low-water flow, m^3/sec.	0.2	0.5
Minimum low-water flow, m^3/sec.	0.12	0.25
Discharge, 50 per cent duration	1.2	—
,, 75 ,, ,, ,,	0.4	—
Percentage of lake	1.8	2.3

Utricularia vulgaris also occur abundantly. The primary production can be assumed to be dominated by the macrophytes and their epiphytes of the bottoms, as is the case in other shallow bodies of water (cf. WETZEL 1964).

During periods of high water in the lake the impoundments are directly connected with it by an outlet channel in the barrier. There is a 75 per cent probability that in the month of July this water level will be reached. In order to safeguard a migration of fish between lake and the impoundments also at a lower water level in the lake there have been constructed fish-ways which open into the lake 2 metres below the crown of the barrier.

3. Results

The quantity and composition of the bottom fauna can be seen in Table 2. The Table does not include the small chironomid larvae and *Bosmina coregoni* BAIRD. which are supposed to suffer the greatest losses in the course of the sifting of the samples (sieves with 0.6 mm mesh). The small chironomid larvae, especially, are very numerous; their inclusion would double the average abundance of the bottom animals, but would only inconsiderably influence the average weight of animals.

Maximum abundance, viz. 12,000 ind./sq. m, has been obtained within the uppermost metres of depth, partly upon naked dy-bottoms, where the larvae of chironomids are strongly dominant, and partly upon bottoms overgrown with *Drepanocladus,* where half of the fauna consists of periphytic cladoceres. Medium abundance, viz. 7,000 ind./sq. m, has been found at greater

Table 2. The bottom fauna of the inlet impoundment (Satsån) of Lake Kultsjön.

Total	Weight, g/sq. m 6.46	Number, ind./sq. m 8,745
	In per cent of the total fauna	
Chironomidae	35.2	64.8
Insecta, excl. *Chir.*	34.9	1.8
Remainder	29.9	—
Cladocera	—	21.9
Oligochaeta	—	4.5
Copepoda	—	3.3
Pisidae	—	3.0
Hydracarina	—	0.5
Nematoda	—	0.1
Ostracoda	—	0.1

depth in organogenic soft bottoms containing mainly chironomids, and minimum abundance, viz. 4,000 ind./sq. m, has been observed in sandy bottoms with a sparse vegetation of *Nitella,* in close connection with the old river channel.

The abundance and biomass of the bottom animals differ somewhat from those found at the corresponding depth in the natural lakes of the region. The average abundance equals the average for the year in Lake Ankarvattnet (GRIMÅS 1961), but surpasses that registered during the same season (June) in the littoral of Lake Kultsjön before the regulation (GRIMÅS 1965). This is connected with some differences in the composition of the fauna.

There is a characteristic dominance of the chironomids in the bottoms in spite of the emergence that is taking place of many species. The wealth of benthic cladoceres is, however, worthy of notice and constitutes a difference. In the littoral of the natural lakes in the region the occurrence of these animals in June is low, and the period of maximum occurrence falls in the month of August. In the impoundments the bottoms covered with vegetation exhibit an abundance of *Eurycercus lamellatus* MÜLL., *Ophryoxus gracilis* SARS, *Alona quadrangularis* MÜLL., and in addition of *Camtocercus rectirostris* SCHOED., *Simocephalus vetulus* MÜLL., and *Iliocryptus acutifrons* SARS. A similar rapid development of zooplankton communities has been observed by ELGMORK (1964) in small, inundated ponds. It is tempting to correlate this development with the temperature which ought to rise faster in the shallow impoundments than in the lake (cf. KREUTNER 1934).

The planktonic crustaceans are dominated by *Bosmina coregoni* BAIRD. Less common are *Daphina hyalina* LEYD., *Holopedium gibberum* ZADD., *Acroperus harpae* BAIRD. and copepodites of *Diaptomus* sp. and *Cyclops* sp.

The chironomid fauna consists to a very large extent of *Tanypodinae* and *Tanytarsini.* Many important species are normally found in the littoral regions of the subarctic lakes (cf. BRUNDIN 1949) even if the chironomid fauna as a whole seems characteristic of shallow bodies of water in the region (cf. THIENEMANN 1942), e.g. the relatively abundance of *Chironomini.* Upon the shallow bottoms pupae of *Ablabesmyia monilis* L. are very common upon the moss-covered surfaces together with larvae of *Procladius,* and upon the naked sedimentary surfaces the *Tanytarsus gregarius* — group and *Paratanytarsus* are abundant. In dy-bottoms at somewhat greater depth, *Chironomus anthracinus* ZETT. becomes more abundant. In addition we may mention species of *Psectrocladius* and *Microtendipes, Heterotrissocladius marcidus* EDW., *Stempellinella minor* EDW. and *Constempellina brevicosta* EDW. Both *Corynoneura cleripes* WINN. and *Chironomus anthracinus* are just emerging and are numerous in the surface of the water and along the shores. Among the flying and swarming animals we may also refer to *Cricotopus alpicola* EDW., *Stichtochironomus rosenschöldi* EDW., and *Limnochironomus pulsus* EDW., which might have derived from the lake.

More remarkable is the occurrence of *Psectrotanypus varius* FABR. (pupae), which in Sweden is otherwise known in the southern parts of the country only (BRUNDIN 1949). Within the rest of its area of dispersal in Europe this species is known, according to FITTKAU (1962), as euroxybiontic and eurythermous but stenotopic and tied to shallow pools, ponds, and tarns, and thus as a biotope comparable to the shallow inlet impoundments of Lake Kultsjön.

The remainder of the insect fauna consists of organisms of greater size, these too, being typical forms of the littoral. As far as numbers are concerned, they do not occupy a conspicuous place in the fauna. On account of their size however, they constitute one third of the biomass of the fauna (Fig. 1), and their availability makes them an important element in the diet of the fish (cf. GRIMÅS 1963). First among these insects we may mention the ephemerids, which are numerous both in the bottom samples and in the stomachs of fish from the impoundments (SASSERSSON, private communication). *Siphlonurus lacustris* ETN. is among the animals characteristic of the high mountain lakes. Together with *Parameletus chelifer* BENGTS. it is abundant in the impoundments in all bottom and is particularly numerous at the very edge of the water, and also upon naked minerogenic sediments. From among the others we may refer to *Ameletus inopinatus* ETN. as well as *Leptophlebia vespertina* L. and *Heptagenia fuscogrisea* RETZ. Most common among the trichopters is *Phryganea obsoleta* MCLACHL., as a species belonging to stagnant waters rich in vegetation. To a similar biotope belong also *Limnephilus despectus* RAMB., *L. fuscicornis* WALK. and *L. centralis* CURT., *Molanna* sp., and larvae of the genera *Rhantus* and *Agabus* from among the *Coleoptera.*

In the immediate vicinity of the inlets the fauna is augmented by more rheophilous forms like *Heptagenia sulphurea* MÜLL., *Ephemerella ignita* PODA, *Isoperla grammatica* PODA, *Polycentropus flavomaculatus* PICT., and *Halesus tesselatus* RAMB., the two last-mentioned as pupae.

Other littoral organisms of major size, which normally occur in the littoral of the natural lakes of the region and often form part of the diet of the fish, seem to be less well-represented in the fauna of the impoundments e.g. the gastropod *Gyraulus acronicus* FÉR., which occurs sparsely in the qualitative material.

Gammarus lacustris SARS, which in the littoral of Lake Kultsjön made up 3 per cent of the total number of individuals before the regulation and accounts for 4 per cent in the neighbouring Lake Ankarvattnet, and which forms a much higher percentage of the biomass, is missing in the material from the inlet impoundments. The reason for its absence cannot be determined with certainty. The investigations into the choice of food by the fish have not yet been concluded, but nothing points towards a decided reduction of the population by predation (SASSERSSON, private communication). Segerstråle (1954) established the absence of *G. lacustris* in waters which are frozen to the bottom in winter. Its distribution in Lake Kultsjön, prior to regulation, seems to extend to deeper regions during the winter, with maximum abundance in the depth zones 0—2 metres in June and 5—7 metres in January (GRIMÅS 1965). An explanation might be found in the assumption that the species is sensitive to the winter temperatures in the shallow impoundments, where it is unable to move to greater depths. In spite of the fact that the level of water does not change throughout the year, it is nevertheless possible that one third of the bottom area freezes, since the ice cover can reach a thickness of up to one metre, and the remaining water is chilled down to about 0°C.

The effect of the conditions in the inlet impoundments reminds one of the extensively regulated Norwegian lakes. In these lakes the availability of organogenic material in the shape of the original terrestrial vegetation seems to enable littoral species of insects of larger size to settle upon the bottom, but, perhaps as a result of the great annual amplitude of the water-level, *Gammarus,* undergoes a total reduction.

The possibility of improving the nutritional conditions for fish in the regulated lakes by inlet impoundments can be regarded as good. Our possibilities of directing production towards desirable kinds of fish are, however, reduced by other factors, first of all the interaction between the various species within the fish fauna. In 1961 the catches in the impoundments consisted to more than 90 per cent of burbot (*Lota lota* L.) (NILSSON 1962). Thus many circumstances suggest that the burbot occupies for the moment a more favourable position in the inlet impoundments of Lake Kultsjön than do the brown trout (*Salmo trutta* L.) and the char (*Salvelinus alpinus* L.).

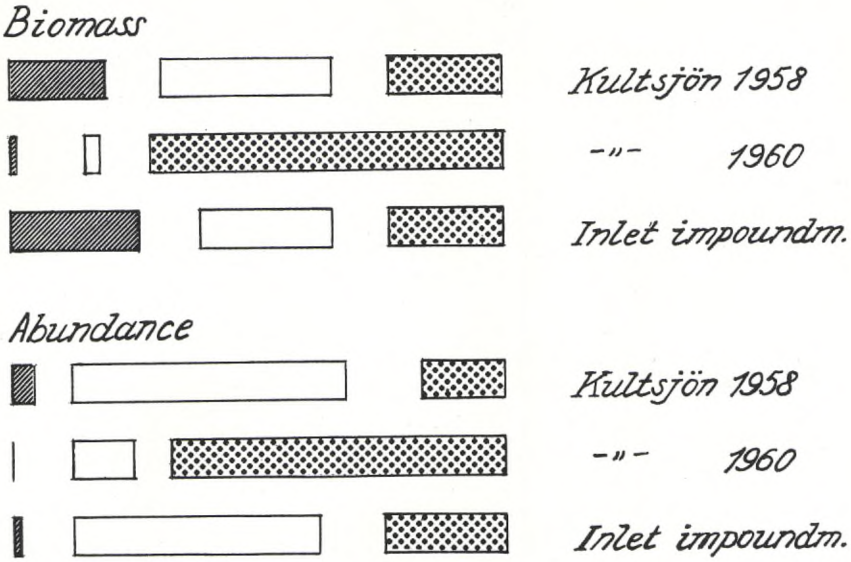


Fig. 1. The composition of the littoral bottom fauna in Lake Kultsjön before (1958) and after (1960) the regulation and in the inlet impoundment of Satsån (1963). Lined: "fish food" organisms such as insect larvae and crustaceans of major size plus gastropods. White: chironomids. Dotted: the remaining components of the fauna.

4. Summary

The inlet impoundments, with their stable water level throughout the year, complement the fauna of the regulated lake with a community of animals that is normally destroyed by the interference. Their special features as distinguished to the natural littoral are connected with their character as shallow bodies of water. Species that can be assumed to depend upon the possibility of migrating towards greater depths during the winter, e.g. *Gammarus lacustris,* seem to be hampered in their development. Through the low temperatures in winter and the fast rise of temperature in spring, the course of the temperature seems on the other hand to stimulate the development of benthic cladoceres. The greatest importance of the inlet impoundments lies, however, in the fact that they preserve to the fish available areas with littoral vegetation and organogenic bottoms and, thereby, areas with a high density of bottom organisms and a balance of species within the fauna which in its main features agrees with that of the original littoral (Fig. 1). As an example may be mentioned the dominance of the insects, many of them being important fish-food organisms.

5. References

AASS, P., 1963. Limingenreguleringens virkninger på fisket. In Norwegian, mimeographed.

BRUNDIN, L., 1949. Chironomiden und andere Bodentiere der Südschwedischen Urgebirgsseen. — *Rep. Inst. Freshw. Res., Drottning., 30,* 1—914.

EIFAC, 1964. Newsletter nr. 2, 23—24.

ELGMORK, K., 1964. Dynamics of zooplankton communities in some small inundated ponds. — *Folia limnol. scand. 12,* 1—83.

FITTKAU, E. J., 1962. Die *Tanypodinae.* — Akademie-Verlag, Berlin, 1—453.

FÜRST, M., 1964. Försök med överföring av nya näringsdjur till reglerade sjöar. — *Inf. Sötvattenslab. Drottning., 7.* In Swedish, mimeographed.

GRIMÅS, U., 1961. The bottom fauna of natural and impounded lakes in Northern Sweden (Ankarvattnet and Blåsjön). — *Rep. Inst. Freshw. Res., Drottning., 42,* 183—237.

— 1962. The effect of increased water level fluctuation upon the bottom fauna in Lake Blåsjön, Northern Sweden. — *Rep. Inst. Freshw. Res., Drottning., 44,* 14—41.

— 1963. Reflections on the availability and utilization degree of bottom animals as fish food. — *Zool. Bidr. Uppsala, 35,* 497—503.

— 1964. Studies on the bottom fauna of impounded lakes in Southern Norway. — *Rep. Inst. Freshw. Res., Drottning., 45,* 94—104.

— 1965. The short term effect of artificial water level fluctuation upon the littoral fauna of Lake Kultsjön, northern Sweden. — *Rep. Inst. Freshw. Res., Drottning., 46,* 5—21.

KREUTNER, W., 1934. Qualitative und quantitative Untersuchungen von Plankton aus schlesischen Versuchteichen (Sulau) auf Grund dreijähriger Probeentnahme. — *Arch. Hydrobiol., 27,* 1—60.

LINDGREN, Ö., 1963. Vattenbeskaffenhet och plankton i Ransaren och Kultsjön. I. Fysikalisk-kemiska förhållanden. — *Rapport fr. Limnol. inst., Uppsala.* In Swedish, mimeographed.

LÖTMARKER, T., 1964. Studies on planktonic crustacea in thirteen lakes in northern Sweden. — *Rep. Inst. Freshw. Res., Drottning., 45,* 113—189.

NILSSON, N.-A., 1961. The effect of water-level fluctuation on the feeding habits of trout and char in the Lakes Blåsjön and Jormsjön, North Sweden. — *Rep. Inst. Freshw. Res., Drottning., 42,* 238—261.

— 1962. Regleringen av Kultsjön och fisket. — *Sv. Fiskeri Tidskr. nr. 6/7,* 94—96. In Swedish.

NILSSON, N.-A. and SVÄRDSON, G., 1962. De nya fiskarna — Försöksverksamheten fram till 31.12.61. — *Inf. Sötvattenslab. Drottning., 1.* In Swedish, mimeographed.

RODHE, W., 1964. Effects of impoundment on water chemistry and plankton in Lake Ransaren (Swedish Lappland). — *Verh. Internat. Verein. Limnol., XV,* 437—443.

RUNNSTRÖM, S., 1951. The population of char, *Salmo alpinus* LINNÉ, in a regulated lake. — *Rep. Inst. Freshw. Res., Drottning., 32,* 66—78.

— 1955. Changes in fish production in impounded lakes. — *Proc. Int. Ass. Theor. Appl. Limn., XII,* 176—182.

SEGERSTRÅLE, S. G., 1954. The freshwater amphipods, *Gammarus pulex* L. and *Gammarus lacustris* G. O. SARS in Denmark and Fennoscandia. — *Soc. Sci. Fenn. Comment. Biol., XV, 1,* 1—91.

SVÄRDSON, G., 1962. See NILSSON.

THIENEMANN, A., 1911. Hydrobiologische und fischereiliche Untersuchungen an den westfälischen Talsperren. — *Landw. Jahrb., 41,* 535—716.

— 1942. Lappländische Chironomiden und ihre Wohngewässer. — *Arch. Hydrobiol., Suppl. bd. XVII,* 1—253.

WETZEL, R. G., 1964. Primary productivity of higher aquatic plants, periphyton and phytoplankton in a large, shallow lake. — *Int. Rev. Hydrobiol., 49,* 1—61.

On the food chain in some north Swedish river reservoirs

ULF GRIMÅS and NILS-ARVID NILSSON

Contents

1. Introduction

International literature dealing with the effects of water power exploitation on fresh water animal communities has mainly dealt with reservoirs formed by the damming-up of rivers (cf. e.g. THIENEMANN 1911, WUNDSCH 1949, SHADIN 1961, FREY 1963).

In Scandinavia the study has been directed mainly towards impounded lakes in the subarctic region (literature reviewed by AASS 1958, LINDSTRÖM 1962, NILSSON 1964, RODHE 1964, RUNNSTRÖM, S. 1964, GRIMÅS 1965). Parallel with these investigations successful work has been carried out with a view to restoring the population of salmon (*Salmo salar* L.) in the Baltic, since the reproduction of this fish has been hindered by the power plants erected in the lower reaches of the rivers (LINDROTH 1958, 1963, CARLIN 1963). During recent years work has been increasingly concentrated around the conditions of the intervening river reservoirs. The present investigation has been carried out in three river systems of Norrland, viz. those of the rivers Indalsälven, Ångermanälven and Umeälven and comprises six reservoirs, which are entered upon the map (Fig. 1). The investigation includes physico-chemical analyses, the bottom fauna, and the food habits of the fish.

2. Environmental conditions

The age of the reservoirs. In connection with the damming-up of the reservoirs, large portions of the neighbourhood are inundated. The effects of this first phase of a new damming-up resemble those observed in impounded lakes. It is, however, probable that the supply of organogenic and minerogenic material from these drowned areas is of importance for the production of the reservoirs during a considerable time. It can therefore be supposed that the age of the reservoir is of great importance for its productive capa-

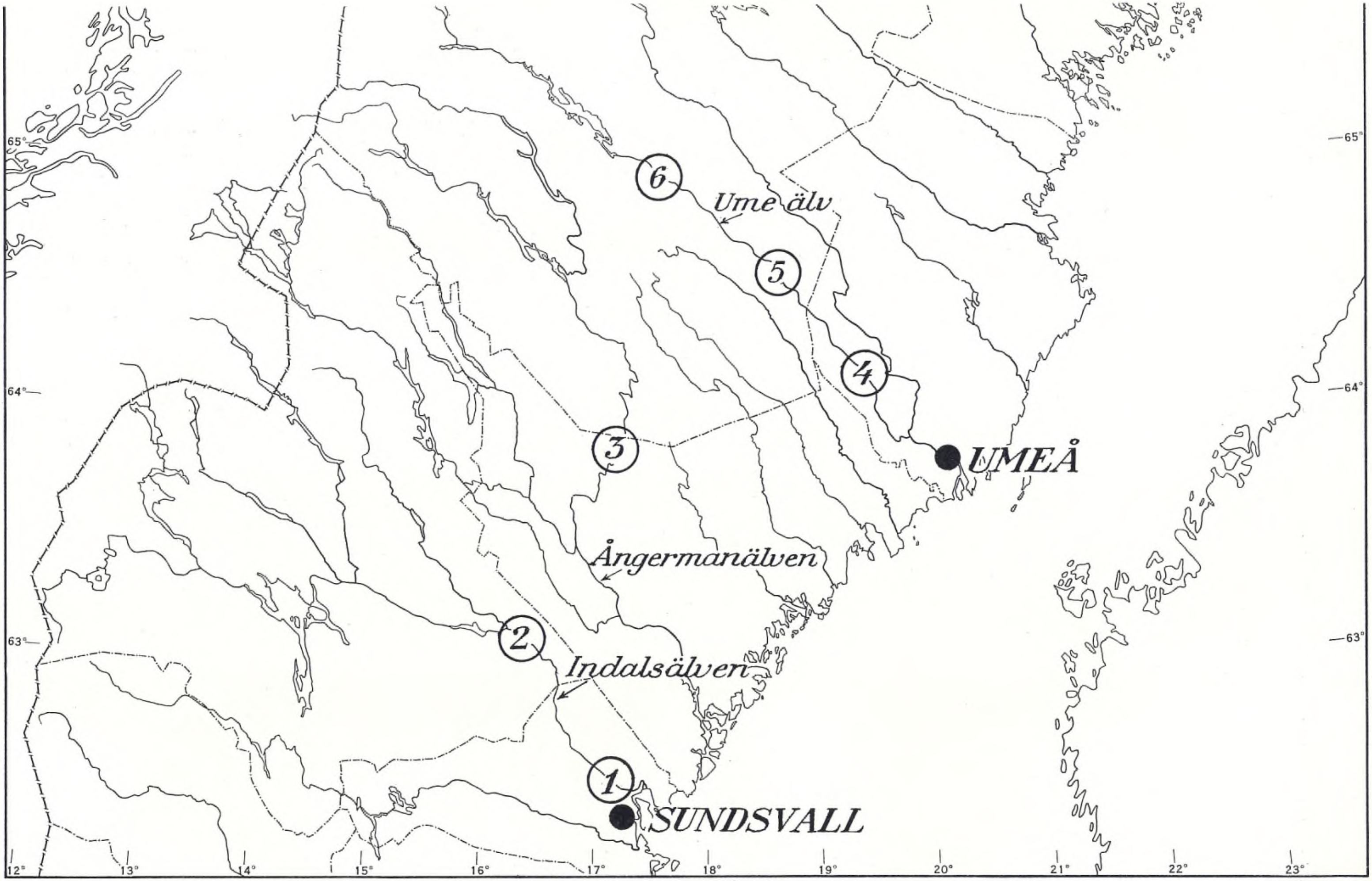


Fig. 1. The geographical situation of the river reservoirs investigated.

Table 1. Data on the reservoirs.

	Start of regulation	Short-time regulation	Amplitude
Indalsälven			
1. Bergeforsen ..	1955	Depends on upstream reservoirs	—
2. Hammarforsen	1928 1943 new damming-up	whole year	0.5—1 m
Ångermanälven			
3. Gulsele	1955	whole year	1.25 m
Umeälven			
4. Bjurfors Övre	1961	1/9—30/4 1964: whole year	1.0 m
5. Rusfors	1962	1/9—20/5 1964: whole year	0.5 m (short-time) 2.3 m (long-time)
6. Grundfors ...	1958	1/9—20/5 1964: whole year	1.0 m

city. This point has been kept in mind in the choice of the objects for the study (see Table 1). Thus the reservoir of Hammarforsen represents a relatively stabilized type, while the reservoirs in Umeälven represent early stages of development.

Physicochemical conditions. The regulation of a river system brings about great changes in the discharge of the river, both annually and diurnally. To the more important changes must be reckoned the increased discharge during winter and the reduced flood in spring. Thus since 1947 the discharge in winter in the lower reaches of the Indalsälven has increased by 100—200 m^3/sec. (BERG 1958). Apart from this, regulations of short duration cause variations connected with a day and night or holidays or weekends. These are most noticeable in the upper parts of the reservoir.

A significant phenomenon with regard to running water is the fact that the velocity of the flow also varies within the mass of water, depending, amongst other things, upon the distance to the bottom (Fig. 2). The velocity of flow is thus greatest immediately below the surface and often diminishes greatly in layers near the bottom.

The establishment of a damming-up area causes increased sedimentation within the area of the river. In regions where previously the current has made for a constant transport of bottom material, the damming amounts to a stabilization. This is exemplified by certain parts of the dammed-up area of Bergeforsen which originally consisted of wandering sandy bottoms but which are now becoming overlain by fine sediments.

According to the observed temperature values (Fig. 3) no stable stratification seems to occur. Even relatively deep reservoirs should be homothermous

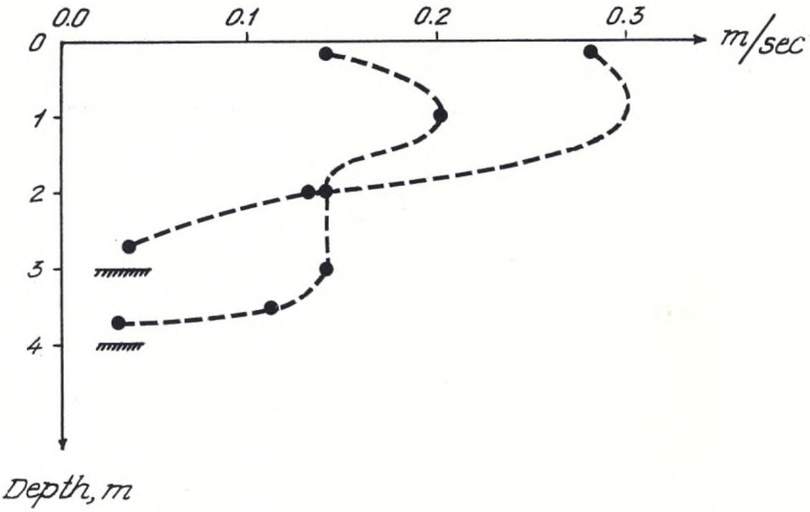


Fig. 2. The various velocity of the water flow at two stations in the Hammarforsen Reservoir.

as a result of the great velocity of flow and the turbulence of water connected with it. The rapid replacement of the water in the reservoir causes both a high temperature in summer and a good supply of oxygen at great depth, which probably exert a positive influence upon the organic production of the reservoir.

The results of the physicochemical samplings in the different reservoirs are given in Table 2. Compared with the other reservoirs, those in Indalsälven exhibit greater transparency and higher values for calcium-magnesium and for electrolytic conductivity. Owing to the presence of humous substances, the water in Gulsele in Ångermanälven is remarkably brown in colour. The humus content also finds its expression in low transparency and pH, a high consumption of permanganate and high Pt-values. The reservoirs of Umeälven are not humified in the same degree, but can on the whole be refered to the same group as Gulsele. The difference in comparison with Indalsälven might include an effect of the recent damming.

River reservoirs versus natural and impounded lakes. The river reservoirs form a very complex environment and their general features are characterized by a far-reaching variation of biotopes from the lake type, which is on the whole found in the lower parts of the reservoirs, to more or less original river conditions still prevailing in the feeding region.

The reservoirs differ fundamentally from the lakes by reason of the rapid changing of their water. As an example can be mentioned the conditions connected with temperature and oxygen and the organic drift, which, amongst

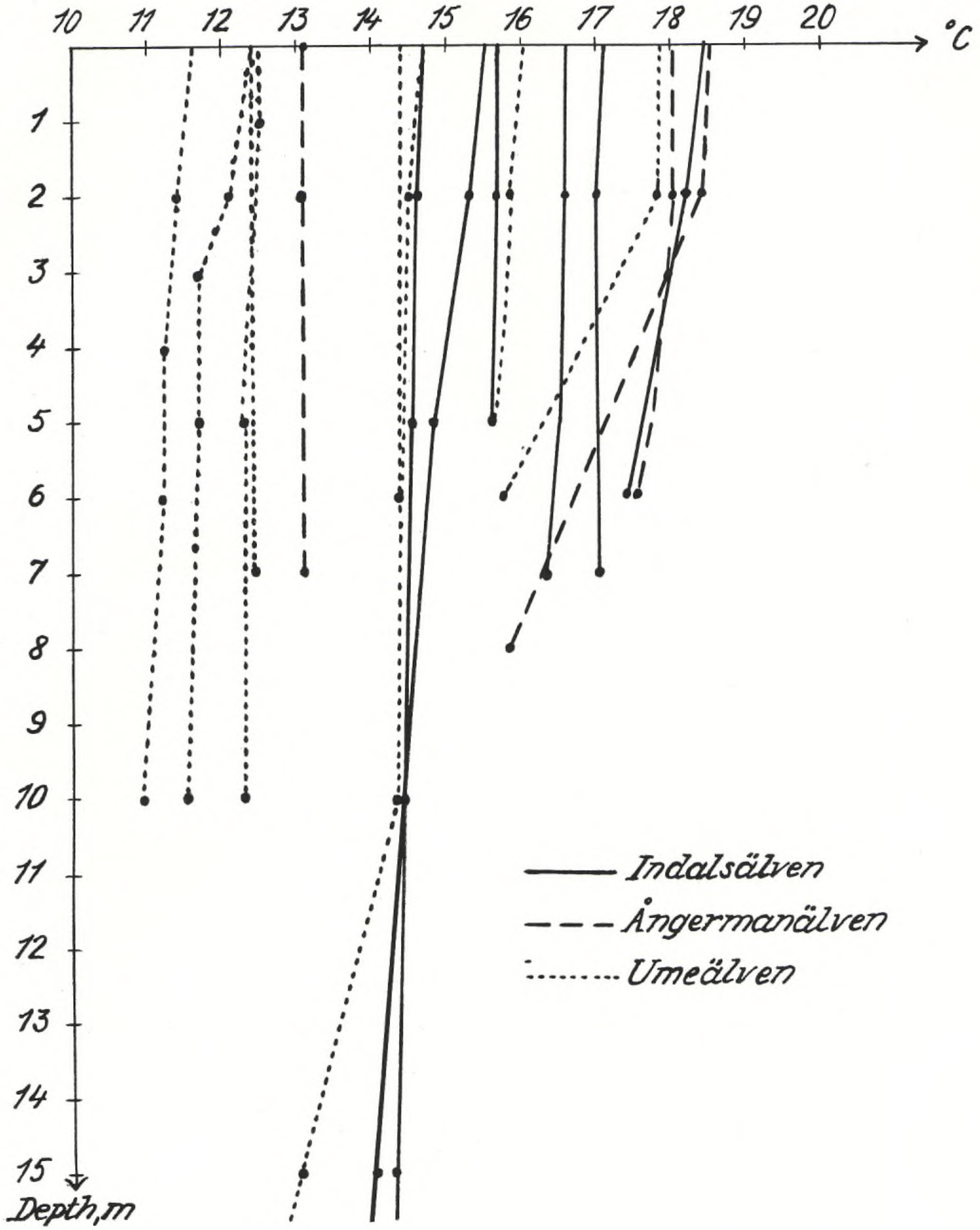


Fig. 3. Temperature conditions in the reservoirs during the months of June, July and August, 1964.

Table 2. Physico-chemical data. (The chemical analyses were made by the National Water Protection Service, Drottningholm.)

		Indalsälven		Ångermanälven	Umeälven		
		Bergeforsen	Hammarforsen	Gulsele	Bjurfors Övre	Rusfors	Grundfors
Transparency	June	4.0	5.2	3.0	—	3.4	3.8
Colour	June	Green yellow	Yellow	Yellow brown	—	Brown yellow	Brown yellow
Colour mg/l Pt	June	25	30	45	35	25	20
	July	30	30	40	21	25	15
	Aug.	20	10	30	15	10	10
$\varkappa \cdot 10^6$	June	43	40	27	27	28	31
	July	43	44	29	32	34	34
	Aug.	46	46	29	32	33	33
pH	June	7.4	7.3	7.1	7.1	7.0	7.3
	July	7.2	7.1	7.0	7.3	7.1	7.3
	Aug.	7.4	7.7	7.2	7.3	7.4	7.4
$KMnO_4$ mg/l	June	19	18	29	27	21	15
	July	22	22	24	—	14	11
	Aug.	18	15	22	16	16	12
Ca+Mg µmol/l	June	196	190	117	125	123	139
	July	202	226	121	129	139	145
	Aug.	222	226	129	140	169	147
Tot. P µg/l	July	10.3	3.6	3.4	2.6	3.2	5.1
Kjelldahl-N. µg/l	July	38	55	26	61	112	26
	Aug.	26	27	84	112	101	26

other things, implies a high and direct introduction of living material at all levels of the water masses.

The most important difference between river reservoirs and impounded lakes is connected with the fluctuations of the water level. In impounded lakes considerable variations of the water level generally occur in the course of the year, the surface being at the damming-up limit in summer and lower in winter. In river reservoirs examined, on the other hand, the annual amplitude of the water is comparatively small in spite of the fact that temporary and rapid changes of level within the predetermined limits can be caused by short-time regulation. As a result of this relatively stable water level and in contrast to what is the cause in the impounded lake, a rich aquatic vegetation can develop within great parts of the reservoir. As an example we can mention the strongly developed belts of *Sparganium* and *Potamogeton* in the Hammarforsen reservoir. The remains of the original terrestrial vegetation are also of importance for production within the inundated areas.

3. The fauna

Earlier investigations into the fauna of river reservoirs in Sweden have concentrated mainly on their feeding regions and the beach which is influenced by the short-time regulation.

MÜLLER (1956, 1958) points, amongst other things, to the negative importance of the low temperature in spring for the fauna of the river below the power-plant reservoirs and to the positive effect of the reservoirs upon this water course as a supplier of nutrition, mainly in the shape of planktonic organisms. BERG (1958) establishes that the short-time regulation influences the fauna within the affected beach zone, but considers that this effect is of small importance. Similar results have been obtained by JOSEFSEN (1953), who examined the reaction of the river fauna to short-time regulations in Norwegian rivers. The number of species and individuals of the faunas of the bottoms is affected only inconsiderably, if at all. Nor does the regulation seem to contribute to any displacement in the life cycle of the species or to any changes in the density of the populations in the succeeding year.

A discussion of the importance of the river reservoirs as feeding environment for a recent or newly introduced fish fauna would not, however, be complete unless the qualitative and quantitative composition of the food fauna in the deeper portions of the reservoir were also taken into consideration. The results set out below indicate that *the bottoms of the reservoirs, irrespective of the depth, can most closely be compared with littoral regions, amongst other things with regard to the availability of organisms suitable as fish food.*

The qualitative composition of the fauna. As a result of the retarded flow of water such characteristic rheophilous forms as simulids have greatly diminished within the region of the river. The altered specific composition is nevertheless characterized by a large number of forms, varying from purely rheophilous organisms to pure lake forms. The "mixed fauna" is especially evident in the central portions of the reservoirs. It might be tempting to refer to the biological structure of the reservoirs as examples of "edge effect" (see Tables 3 and 4). The main part of the fauna consists of species known for their extensive tolerance with regard to environmental factors, yet the same bottom samples contain species that can be regarded as typical of the environments of both lakes and running water. Thus in Hammarforsen, for instance, we find *Mysis relicta, Pallasea quadrispinosa,* and *Constempellina brevicosta* together with a fauna of river character. In Gulsele species of rheophilous insects occur in samples containing a fauna which is dominated by pisids, oligochaetes and benthic cladoceres. In Bjurfors Övre dense swarms of *Polyphemus pediculus* occur along beaches with high abundance of *Neureclipsis bimaculata.*

The fauna of the feeding regions is characterized by rheophilous species.

Table 3. The occurence of gastropods and aquatic insects in the reservoirs. Number of ×=number of reservoirs.

	Feeding regions	Other regions
Gastropoda		
Lymnæa palustris Müll.	—	××
— *peregra* Müll.	××	×××
Planorbis planorbis L.	××	×
— *carinatus* Müll.	—	×
Gyraulus albus Müll.	—	×
— *acronicus* Fer.	×××	××××
Valvata macrostoma Steenb.	—	××××
Ephemeroptera		
Ephemera vulgata L.	—	×
— *danica* Müll.	—	×××
Caenis horaria L.	×	××
— *rivulorum* Etn.	××	—
— *macrura* Steph.	—	×
Ephemerella ignita Poda	—	×
— *notata* Etn.	×	××
Athroplea congener Bengts.	—	×
Heptagenia sulphurea Müll.	×××	—
— *fuscogrisea* Retz.	××	×
— sp.	××	—
Leptophlebia vespertina L.	×	××
Metretopus sp.	××××	—
Ameletus inopinatus Etn.	—	×
Siphlonurus linneatus Etn.	×	××
— *lacustris* Etn.	×	×××
Centroptilum luteolum Müll.	××	××××
Cloeon dipterum L.	—	××
— *simile* Etn.	—	××
Baetis scambus Etn.	×	—
— *rhodani* Pict.	×	—
— sp.	—	×××
Odonata		
Ishnura conf. *elegans* Vand.	—	×
Plecoptera		
Nemoura cinerea Retz.	—	×
Leuctra fusca L.	—	×
Diura bicaudata L.	—	×
Isoperla grammatica Scop.	×	—
— *obscura* Zett.	××	××
Chloroperla burmeisteri Pict.	××	×
Heteroptera		
Cymatia conf. *bonsdorffi* C.Sb.	—	×
Corixa sp.	—	×
Sigara sp.	—	×
Megaloptera		
Sialis lutaria L.	—	×
Trichoptera		
Hydroptila femoralis Eat.	×	—
— sp.	—	×

Table 3. Continued.

	Feeding regions	Other regions
Agraylea sp.	—	×
Oxyethira costalis CURT.	—	×
Neureclipsis bimaculata L.	××	××
Cyrnus trimaculatus CURT.	—	×
Polycentropus flavomaculatus CURT.	—	×
Hydropsyche pellucidula CURT.	××	—
— *angustipennis* CURT.	×	—
Phryganea obsoleta McLACHL.	—	×
— sp.	—	×
Molanna angustata CURT.	×	××
— sp.	—	×××
Molannodes zelleri McLACHL.	—	×
Athripsodes annulicornis STEPH.	×	—
— *cinereus* CURT.	××	×
— sp.	×	××
Mystacides nigra L.	—	×
— *azurea* L.	×	×××
Anabolia nervosa LEACH.	×	×
Limnephilus rhombicus L.	—	×
— *borealis* ZETT.	—	×
— ssp.	×	××
Stenophylax infumatus McLACHL.	××	—
Halesus tesselatus RAMB.	—	××
— *digitatus* SCHRK.	×	—
Apatania sp.	×	—
Lepidostoma hirtum FABR.	—	×
Sericostomatidae	×	—
Coleoptera		
Haliplus fulvus FABR.	×	—
— *lineatocollis* MARSH.	—	×
Hydroporus sp.	××	×
Deronectes depressus FABR.	—	×
— *halensis* FABR.	×	—
— sp.	×	—
Platambus maculatus L.	—	×
Agabus conspersus MARSH.	—	×
— *sturmi* GYLL.	—	×
Rhantus scutellatus HARR.	—	×
Colymbetes fuscus L.	—	××
Dryops sp.	—	×
Helmiinae	—	××
Diptera		
Constempellina brevicosta EDW.	—	××××
Simulium morsitans EDW.	×	—
— *venustrum* SAY.	×	—
— ssp.	××	—

As examples can be mentioned *Simulium morsitans, S. venustum, Hydropsyche angustipennis, H. pellucida, Baetis scambus, B. rhodani,* and swarming *Hydropsychae nevae* and *Agapetus comatus* in the upper reaches of Bergeforsen. In the feeding region of Bjurfors Övre occur *Simulium* sp., *Rheotanytarsus* sp., *Chloroperla burmeisteri, Caenis rivulorum, Neureclipsis*

Table 4. *Trichoptera.* Imagines along the shores of the reservoirs. Examined by prof. C. H. Forsslund.

Hammarforsen		
Barrage site, spring:	*Lype phaeopa* Steph.	
	Hydropsyche contubernalis McLachl.	
autumn:	*Athripsodes cinereus* Curt.	
Bergeforsen		
Feeding region:	*Diploglossa nylanderi* McLachl.	
	Agapetus comatus Pict.	numerous
	Hydropsyche nigronervosus Retz.	
	— *nevae* Kol.	swarming
Barrage site:	*Neureclipsis bimaculata* L.	
	Hydropsyche nevae Kol.	
	Athripsodes nigronervosus Retz.	numerous
	— *perplexus* McLachl.	,,
Gulsele		
Feeding region:	*Agapetus comatus* Pict.	
	Polycentropus flavomaculatus Pict.	
	Molanna angustata Curt.	
	Micrasema nigrum Br.	
	Athripsodes annulicornis Steph.	
	— *perplexus* McLachl.	numerous
Barrage site:	*Polycentropus multiguttatus* Curt.	
	Athripsodes nigronervosus Retz.	
	— *perplexus* McLachl.	egg-laying
Rusfors		
Feeding region:	*Apatania wallengreni* McLachl.	swarming
Grundfors		
Stream:	*Arctopsyche ladogensis* Kol.	
	Apatania wallengreni McLachl.	swarming
Barrage site:	*Nemotaulius punctatolineatus* Retz.	
	Limnephilus rhombicus L.	
	Apatania wallengreni McLachl.	numerous

bimaculata and *Hydropsyche pellucida,* at Grundfors are found *Archtopsyche ladogensis,* a pronounced rheophilous form typical for northern rivers, and at Gulsele *Stenophylax infumatus, Agapetus comatus* and *Micrasema nigrum.*

The lower parts of the reservoirs and other regions of lake character contain in their depths a fauna which in many respects resembles that of a natural lake, i.e. which is dominated by oligochaetes, pisids, and chironomids. An important difference from the fauna of the lake is, however, constituted by the fact that together with these profundal organisms there occur species which usually are restricted to the littoral, e.g. large crustaceans, large insect larvae and gastropods. Among the bottom animals which seem to be especially favoured by the damming-up *Pallasea quadrispinosa* may be mentioned. The abundant occurence of this important fish food organism is probably connected with the circumstance that this species, in contrast to e.g. *Gammarus,* is capable of utilizing deeper water also. Investiga-

Table 5. The percental share of small crustaceans in the bottom fauna in reservoirs of various ages of regulation. Depth zone 8—10 metres.

Reservoir	Year of damming-up	Small crustaceans	Remainder	Dominant forms
Rusfors	1962	80	20	cladoceres copepods
Grundfors	1958	20	80	chironomids oligochaetes pisids
Bergeforsen	1955	15	85	chironomids
Hammarforsen	1928	5	95	chironomids pisids oligochaetes

tions by S. E. BERG (private communication) showed *Gammarus* to dominate in the unregulated Vindelälven. Furthermore can be mentioned the occurence in Bergeforsen of *Valvata macrostoma* and *Gyraulus acronicus* down to a depth of 23 metres, of *Neureclipsis bimaculata, Asellus aquaticus, Gyraulus acronicus* and *Caenis* sp. in Hammarforsen, of *Baetis, Neureclipsis* and larvae of *Helmiinae* in Rusfors and of *Gyraulus albus, Molannodes zelleri,* and *Athripsodes cinereus* in Grundfors, all of them down to a depth of 10 metres. At slightly smaller depth, 7—10 metres, there normally occur e.g. *Asellus aquaticus, Valvata macrostoma, Ephemera vulgata, E. danica, Ephemerella notata, Oxyethira costalis,* and *Limnephilus rhombicus,* together with *Mystacides* sp. and *Oecetis* sp. In all reservoirs the littoral fauna is very rich in species as far down as 7 metres. As examples can be mentioned *Polycentropus multiguttatus* in Gulsele and *Lype phaeopa* in Hammarforsen, species which in these northern regions are considered rare (FORSSLUND, communicated by letter).

The occurance of littoral animals in all depth zones can be ascribed to the extensive flow of water and factors connected therewith. In contrast to the rigid zonation of the lakes in littoral and profundal regions the reservoirs exhibit equalizing conditions in favour of the littoral organisms. *This eurybathic distribution of littoral animals in the river reservoirs diminishes the relative importance of the upper littoral as feeding ground for the fishes and thus also the effect of the short time regulation.*

In the youngest reservoirs the effect of the damming-up is noticeable by the occurence of dense swarms of semipelagic cladoceres like *Eurycercus lamellatus, Sida crystallina,* and *Polyphemus pediculus.* In this respect the young reservoirs agree with recently impounded lakes. The share of small crustaceans (cladoceres, copepods and ostracodes) in the fauna of the different reservoirs is evident from Table 5.

The quantity of bottom animals. The quantitative results are shown in Table 6. The distribution of the animals with regard to depth agrees on the

Table 6. Hammarforsen Reservoir. The bathymetrical distribution of bottom animals and the percental share of various groups of animals in the total fauna. "Fish food" organisms include major crustaceans and insects plus gastropods. The remaining large animals, such as *Anodonta* and *Petromyzon fluviatilis* are included in "Remainder". This material does not comprise areas in the reservoir with stream velocity exceeding 0.2 metres per second.

Depth m	Number of ind./sq.m.	"fish food"	Chir.	Olig.	Pis.	Small Crust.	Remaind.	Biotope
2	45,056	2	10	38	7	37	6	Lake type+ vegetation
3	16,412	13	37	22	6	20	2	slow stream type+*Nitella*
5	6,966	17	36	17	17	8	5	slow stream dy+bark
7	7,861	1	13	46	30	3	7	lake type naked sedim.
9	12,804	8	30	19	30	11	2	slow stream 0.2 m/sec. in surface, dy
10	12,041	1	28	37	30	3	2	lake type dy

whole with the conditions in a lake, i.e. the maximum abundance is found in shallow bottoms. In the reservoir of Hammarforsen an abundance of 45,000 ind./sq. m has been noted for the uppermost metres of depth. For the depth zone 0—10 metres the average density amounts to 16,768 ind./sq. m of which 909 individuals are fish food organisms of larger size. This concentration must be regarded as very high. Particular notice is merited by the high concentration of fish food organisms and chironomids in fairly agitated waters, the dominance of the oligochaetes in the lake-like portions, and the great number of periphytic animals, like cladoceres, in connection with the vegetation.

Composition of the fish fauna. A great number of test fishing operations, the results of which are accounted for in mimographed reports from the Institute for Fresh Water Research, the Local Fisheries Administration, and the Hydroelectric Power Board, show that with the building of power plants and dams for water-power exploitation the composition of the fish fauna undergoes characteristic changes. Table 7 (after RUNNSTRÖM, H. 1964) gives a characteristic example of the catch in one of the reservoirs examined, viz. Gulsele, standard sets of gill nets having been employed. *Migratory salmonids that spawn in running water, like brown trout (Salmo trutta L.), salmon, and grayling (Thymallus thymallus L.), become much rarer or disappear.* Of these species it is only the grayling which has shown the ability to form populations of reasonable importance, and which survives in many reservoirs, especially in their feeding regions. Some kinds of fish, on the

Table 7. Gill net catch in Gulsele Reservoir 1962. (After H. RUNNSTRÖM 1964.)

Month	Number of efforts	Number & kg per effort	White-fish	Pike	Perch	Roach	Burbot	Ide	Sum
May	64	Number	0.18	0.97	2.25	4.67	0.09	0.02	8.18
		Kg	0.09	0.58	0.17	0.34	0.07	0.01	1.26
June	152	Number	0.11	0.36	1.93	5.39	—	—	7.79
		Kg	0.05	0.22	0.17	0.36	—	—	0.80
July	224	Number	0.03	0.27	2.61	2.33	—	—	5.24
		Kg	0.01	0.15	0.21	0.18	—	—	0.55
Aug.	216	Number	0.24	0.43	2.87	2.27	—	—	5.81
		Kg	0.08	0.27	0.24	0.19	—	—	0.78
Sept.	80	Number	0.58	0.21	1.00	1.09	0.21	—	3.09
		Kg	0.18	0.13	0.10	0.11	0.13	—	0.65
Oct.	152	Number	0.77	0.24	1.06	2.68	0.16	—	4.91
		Kg	0.23	0.18	0.09	0.23	0.10	—	0.83
Sum	888	Number	0.32	0.41	1.95	3.07	0.08	< 0.01	5.83
		Kg	0.11	0.26	0.16	0.24	0.05	< 0.01	0.82

other hand, assume increased importance. Some species, e.g. whitefish (*Coregonus*), exhibit in isolated cases (Gulsele) a tendency towards increased representation in the catches; in other cases they become rarer, but still constitute populations of some importance. *The species which regularly seem to form denser populations are roach (Leuciscus rutilus L.), perch (Perca fluviatilis L.) and pike (Esox lucius L.).* These tendencies on the whole agree with experiences derived from other parts of Europe (cf. WUNDSCH 1949, SCHADIN 1961, STARMACH 1961). A contributory cause for this development, which is unfavourable from the point of view of the fisherman, consists in the fact that the difficulties encountered in fishing often result in partial or total cessation of all fishing activities.

The percentage of the different species of fish in the test fishing operations in Hammarforsen, Gulsele, and Bjurfors Övre can be seen from Table 8, which provides a good illustration of the conditions accounted for above. It is worth while to notice the dominance of pike and whitefish in the youngest reservoirs, and that of roach and perch in the oldest. The changes in the composition of the fish fauna do not seem to be due to an adverse influence of the sudden changes in the water flow upon reproduction (LINDROTH 1955, BERG 1958). In addition to the fact that the species of fish which migrate into the sea are prevented by the construction of the power plants from reaching the places for their spawning and juvenile development, the above mentioned changes must be due to other causes, e.g. food production, predation, competition, etc.

The food habits of the fish. The food habits of the different species of fish in Hammarforsen, Gulsele and Bjurfors Övre can be seen from Table 9, 10, 11 and 12. Apart from the pike, which in the reservoirs as elsewhere is a fish-eater, all the other species of fish examined draw the most impor-

Table 8. The species composition of the fish fauna according to test fishing data from three reservoirs. Figures given as per cent of total catches.

	Trout	Grayling	Whitefish	Smelt	Pike	Perch	Ruff	Burbot	Roach	Dace	Ide
Hammarforsen											
1964 . . . . . 105 efforts	0.25	0.7	7.8	0.5	7.5	26.8	6.6	—	48.1	1.8	—
Gulsele											
1962 . . . . . 888 efforts	—	—	5.5	—	7.0	33.4	—	1.4	52.7	—	< 0.1
Bjurfors Övre											
July—Aug. 1963 . . . . . 608 efforts	0.4	2.1	10.8	—	5.6	57.9	0.4	0.05	1.9	20.9	—
Bjurfors Övre											
Oct.—Nov. 1963 . . . . . 512 efforts	0.1	4.1	32.6	—	14.2	30.7	10.8	—	3.8	3.7	—

tant component of their food from among the bottom animals. The planktonic crustaceans are of importance only for the small whitefish in Bjurfors Övre, a fact which can be assumed to be connected with the flourishing of minor crustaceans in the recently dammed-up reservoirs.

Among the bottom animals it is in the first instance the insects, major crustaceans and molluscs that are utilized. In two cases, viz. the whitefish in the Hammarforsen reservoir and the grayling in the Gulsele reservoir, the chief food consists of terrestrial insects that have capsized upon the surface of the water. The oligochaetes which are an important component of the bottom fauna are hardly utilized at all by the fish. Among the aquatic insects the major forms, like ephemerids, plecopters, and odonates, are dominant. The chironomids are of importance particularly for the whitefish. Apart from the whitefish which utilize the pisidians, the gastropods (*Lymnæa, Gyraulus*) dominate among the molluscs. Among the major crustaceans *Pallasea quadrispinosa* is especially noticeabel. It is of interest that *Mysis relicta* is also found among the prey.

To sum up, it can be established that the richly diversified supply of food in the reservoirs is paralleled by the food habits of the population of fish inhabiting the waters, i.e. the food spectrum of the fish is extremely broad. On the whole the grayling feed on the organic drift in the inflow regions (simulids, terrestrial insects, larvae of ephemerids and trichopters), the whitefish on plankton and sediment organisms (pisids, chironomids, larvae of trichopters and *Pallasea*), the roach on plants and bottom animals, while the pike is a predator, feeding on burbot (*Lota lota* L.), perch, roach, and larvae of odonates and ephemerids.

In the material examined there is nothing to indicate that the nutritive conditions as such in the river reservoirs are responsible for the decline of the salmonid species. Their marked decrease in comparison with other species of fish ought rather to be viewed against the background of the above-described change of the environment from lotic to more lake-like conditions, the latter favouring species adapted to them at the expence of the salmonids. An important factor that is adverse to the salmonids is the recruitment of the pike, which for a long time should be favoured by the structure of the drowned bottoms. The complicated environment of the reservoirs, characterized amongst other things in the rate of flow of the water, both in space and time, also seem to favourize the pelagic, roaming species, adapted to life in lakes, in relation to the territorial salmonids. The phenomenon, observed by Lindroth (1955) and Kalleberg (1958), that a change in the velocity of the current the fry of trout and salmon change from territorial to pelagic habits ought also to contribute to the circumstance that they easily become the prey of predators in this special environment.

Table 9. Stomach contents of whitefish and roach in Hammarforsen Reservoir 1963. Expressed as mean percentages of stomach volumes.

Food	July		September		October	
	Whitefish	Roach	Whitefish	Roach	Whitefish	Roach
Fish remains	—	—	—	1.0	—	—
Daphnia	+	—	—	—	—	—
Eurycercus	+	—	13.6	0.8	—	—
Cyclops	+	—	+	+	—	—
Ostracoda	0.6	—	+	—	—	—
Plankton remains	—	+	—	—	—	2.9
Asellus aquaticus	—	—	—	—	0.5	—
Pallasea	+	5.9	4.7	0.6	13.1	—
Gastropoda	—	6.1	—	31.2	—	—
Planorbidae	7.2	—	14.3	—	2.8	—
Lymnaea	—	—	6.3	—	10.7	—
Valvata	—	—	—	3.5	—	—
Sphaeriidae	15.0	—	19.3	—	25.2	—
Chironomidae l.	7.0	0.2	4.3	0.5	11.7	—
— p.	4.6	—	—	—	—	—
Ceratopogonidae l.	+	+	+	—	+	—
Ephemeroptera l.	+	—	+	—	—	—
— p.	1.9	—	—	—	—	—
Trichoptera l.	2.3	19.2	3.9	1.1	0.9	10.6
— p.	1.6	—	—	—	—	—
— i.	1.3	—	—	—	—	—
Terrestrial insects	32.7	4.4	11.1	0.2	7.3	5.8
Acantocephala	—	—	—	0.2	—	—
Cristatella	—	—	+	1.9	0.3	—
Nematoda	0.9	—	—	—	—	—
Hydracarina	+	+	—	0.1	—	—
Algae	—	13.8	—	8.5	—	1.2
Plants	7.6	5.0	7.0	3.0	6.1	0.1
Minerogenic particles	5.1	1.2	6.3	0.7	0.8	—
Organogenic and minerogenic mud	12.2	44.3	9.3	46.9	20.6	79.4

Table 10. Stomach contents of whitefish, pike, and grayling in Gulsele Reservoir 1962.

Food	May		June		July		August		September		October		July, Aug., Oct.
	Whitefish	Pike	Whitefish	Pike	Whitefish	Pike	Whitefish	Pike	Whitefish	Pike	Whitefish	Pike	Grayling
Fish eggs	—	—	—	0.2	—	—	—	—	—	—	7.2	—	—
Fish remains	—	—	—	2.6	—	5.6	—	29.3	—	65.7	—	16.7	5.6
Perch	—	8.6	—	5.6	—	—	—	6.8	—	—	—	—	—
Burbot	—	4.3	—	9.2	—	—	—	—	—	22.2	—	16.7	—
Roach	—	13.6	—	5.3	—	10.9	—	4.9	—	—	—	—	—
River lamprey	—	4.5	—	—	—	—	—	—	—	—	—	—	—
Daphnia	—	—	—	—	—	—	—	0.1	2.0	—	—	—	1.0
Eurycercus	—	—	0.1	—	—	—	0.2	0.2	2.3	—	2.5	—	6.4
Ostracoda	—	—	—	—	—	—	0.1	—	0.8	—	0.4	—	—
Cyclops	—	—	0.1	—	—	—	2.5	—	1.0	—	0.2	—	—
Lymnaea	19.2	—	7.2	—	—	—	8.3	—	0.1	—	7.7	—	8.9
Planorbidae	—	—	1.3	—	—	—	7.1	—	—	—	0.8	—	—
Sphaeriidae	0.3	—	7.9	—	—	—	7.6	—	17.4	—	17.5	—	1.3
Chironomidae l.	3.0	—	8.3	—	45.0	0.4	9.4	—	10.6	—	33.5	—	2.7
— p.	16.7	—	6.0	0.4	—	—	32.0	0.5	2.6	—	—	—	3.4
Ceratopogonidae l.	2.3	—	6.4	—	—	—	1.6	—	1.2	—	0.6	—	—
Simuliidae l.	—	—	1.7	—	—	—	—	—	—	—	—	—	9.1
— p.	—	—	—	—	—	—	—	—	—	—	—	—	2.9
Ephemeroptera l.	43.7	14.9	43.6	33.0	—	4.6	0.3	7.1	6.9	0.7	4.4	—	9.5
Plecoptera l.	0.2	0.9	—	—	—	—	1.7	—	2.4	—	—	—	1.0
Trichoptera l.p.	0.2	0.4	5.7	—	—	11.7	1.3	3.4	21.5	—	—	—	10.4
Dytiscidae l.	—	—	0.5	—	—	—	0.3	—	—	—	—	—	—
Odonata l.	—	—	—	19.5	—	20.0	—	—	—	—	—	—	0.1
Oligochaeta	—	—	1.7	—	—	—	—	—	—	—	0.7	—	—
Trematoda[1]	—	39.5	—	13.0	—	41.6	—	30.2	—	11.3	—	66.7	—
Nematoda	—	3.2	—	5.5	—	—	—	1.6	—	0.1	—	—	6.8
Chironomidae i.	—	—	—	0.1	—	—	5.8	—	—	—	—	—	3.2
Trichoptera i.	—	—	—	—	—	—	—	2.1	—	—	—	—	0.1
Dytiscidae i.	0.5	—	—	—	—	—	—	—	—	—	—	—	—
Corixa i.	0.6	—	—	—	—	—	—	—	0.1	—	0.2	—	—
Coleoptera i.	—	—	—	—	—	—	0.1	—	—	—	—	—	1.1
Hymenoptera i.	—	—	—	—	—	—	—	—	—	—	—	—	6.7
Terrestrial insects	—	—	—	—	—	—	0.2	—	—	—	—	—	18.8
Plants	13.3	6.0	9.3	5.7	55.0	5.3	18.9	13.2	30.7	—	24.4	—	0.9
Miscellaneous	—	4.5	0.1	—	—	—	2.7	—	0.2	—	—	—	—

[1] Parasites (*Azygia lucii*).

Table 11. The stomach contents of whitefish of various size in Gulsele Reservoir 1962.

Food	Size		
	201—300 mm	301—400 mm	> 400 mm
Fish eggs	—	2.6	—
Daphnia	2.1	—	—
Eurycercus	0.8	2.0	0.3
Ostracoda	—	0.8	0.1
Cyclops	2.3	0.1	—
Lymnaea	—	6.0	25.0
Planorbidae	—	0.6	12.1
Valvata	—	—	0.1
Sphaeriidae	17.5	7.6	7.7
Chironomidae l.	14.5	15.6	6.9
— p.	10.7	5.8	14.4
Ceratopogonidae l.	2.1	2.3	0.1
Simuliidae l.	0.7	—	0.1
Ephemeroptera l.	22.3	8.7	12.0
Plecoptera l.	—	2.2	0.1
Trichoptera l.	5.5	13.2	0.1
Dytiscidae l.	—	0.1	0.4
Oligochaeta	—	0.7	—
Chironomidae i.	—	3.1	—
Dytiscidae i.	0.1	0.1	—
Corixa i.	0.2	0.1	—
Terrestrial insects	—	0.1	—
Plants	19.4	28.2	20.1
Minerogenic components	1.4	0.1	0.1

Table 12. Stomach contents of whitefish of various size in Bjurfors Övre Reservoir 1963.

Food	Size		Month	
	201—300 mm	301—400 mm	August	October
Bythotrephes	10.5	0.5	10.9	—
Bosmina	5.3	—	—	6.7
Daphnia	9.6	—	5.8	4.8
Eurycercus	4.8	—	—	6.1
Holopedium	4.2	—	4.2	—
Cyclops	6.7	—	0.5	7.7
Heterocope	—	6.7	5.3	—
Ostracoda	1.7	—	—	2.1
Mysis	5.0	—	5.0	—
Pallasea	10.5	15.8	10.5	15.8
Lymnaea	—	18.7	7.2	9.6
Pisidium	0.3	6.7	0.3	6.7
Planorbidae	—	17.7	8.6	6.9
Sphaeriidae	5.3	6.1	4.8	6.7
Chironomidae l.	34.9	6.7	—	11.9
— p.	—	1.0	0.8	—
Ephemeroptera l.	0.3	—	—	0.3
Plecoptera l.	1.1	—	—	—
Trichoptera	—	13.4	36.1	8.0
Plants	—	6.7	—	6.7

4. References

AASS, P., 1958. The effect of impoundment on inland fisheries. — *Proc. Internat. Union for Conservation of Nature and Natural Resources. RT 7, Id 12,* 9 pp.

BERG, S. E., 1958. Angående korttidsreglering vid Stadsforsen. — Yttrande till Mellanbygdens Vattendomstol den 12 februari, 1958. In Swedish, mimeographed.

CARLIN, B., 1963. Laxforskningsinstitutet och dess hittillsvarande verksamhet. — *Svenska Vattenkr. Fören. Publ., 502,* 223--259. In Swedish. (English summary.)

FREY, D. G., 1963. Limnology of North America. — Madison. 1—734.

GRIMÅS, U., 1965. Effects of impoundments on the bottom fauna of high mountain lakes. — *Acta Universitatis Upsaliensis 51,* in press.

JOSEFSEN, E., 1953. Reguleringsundersökelser i Tisleia, Flya og Nöra I. Bunnfaunaen i Tisleia, Flya og Nöra. Virkninger av kortvarige variasjoner i vannföringen. In Norwegian, mimeographed.

KALLEBERG, H., 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *Salmo trutta* L.). — *Rep. Inst. Freshw. Res., Drottningholm 39,* 55—98.

LINDROTH, A., 1955. Distribution, territorial behaviour and movements of sea trout fry in the River Indalsälven. — *Rep. Inst. Freshw. Res., Drottningholm 36,* 104—119.

— 1958. Anadromous fish conservation in a Swedish salmon river. — *Proc. Internat. Union for Conservation of Nature and Natural Resources. RT 7, Id 21.* 1—9.

— 1963. Salmon conservation in Sweden. — *Trans. Amer. Fish. Soc., 92,* 286—291.

LINDSTRÖM, T., 1962. Life history of whitefish young (*Coregonus*) in two lake reservoirs. — *Rep. Inst. Freshw. Res., Drottningholm, 44,* 113—144.

MÜLLER, K., 1956. Jämförande undersökningar över bottenfaunans kvalitativa och kvantitativa bestånd i reglerade och oreglerade älvar. — *Fiskeribiologiska Medd. fr. Norrbotten, 7.* In Swedish, mimeographed.

— 1958. Om vattentemperaturen i reglerade älvsystem. — *Fiskeribiologiska Medd. fr. Norrbotten, 17.* In Swedish, mimeographed.

NILSSON, N.-A., 1964. Effects of impoundments on the feeding habits of brown trout and char in Lake Ransaren (Swedish Lappland). — *Verh. Internat. Verein. Limnol., XV,* 444—452.

RODHE, W., 1964. Effects of impoundment on water chemistry and plankton in Lake Ransaren (Swedish Lappland). — *Verh. Internat. Verein. Limnol., XV,* 437—443.

RUNNSTRÖM, H., 1964. P.M. den 27 april, 1964, angående fisket i kraftverksmagasin i Ångermanälven. In Swedish, mimeographed.

RUNNSTRÖM, S., 1964. Effects of impoundments on the growth of *Salmo trutta* and *Salvelinus alpinus* in Lake Ransaren (Swedish Lappland). — *Verh. Internat. Verein. Limnol., XV,* 453—461.

SCHADIN, W. I., 1961. Die Wirkung von Stauanlagen auf natürliche Gewässer. — *Verh. Internat. Verein. Limnol., XIV,* 792—805.

STARMACH, K., 1961. Hydrobiologische Untersuchungen an der Talsperre bei Goczalkowice. — *Verh. Internat. Verein. Limnol., XIV,* 643—646.

THIENEMANN, A., 1911. Hydrobiologische und fischereiliche Untersuchungen an den westfälischen Talsperren. — *Landw. Jahrb., 41,* 535—716.

WUNDSCH, H. H., 1949. Grundlagen der Fischwirtschaft in den Grosstaubecken. — *Abh. a. d. Fischerei, N.F. Bd 1,* 17—186.

The composition of the bottom fauna in two basins of Lake Mälaren

By Tom Åhrén and Ulf Grimås

Institute of Zoology, Entomological Department, Uppsala

Contents

1. Introduction

The bottom fauna has been studied in two basins of Lake Mälaren, Central Sweden, viz. in L. Ullevifjärden and in Ekoln. Both are situated in the north-eastern part of the lake and are separated from other portions of the lake by narrow sounds. On this account they can be regarded as independent lakes from the biological point of view (cf. Ekman 1907).

Both L. Ullevifjärden and Ekoln are eutrophic (cf. Lohammar 1938) with well-developed profundals (maximum depth 58 and 50 metres, respectively). They have a well-developed temperature stratification in summer and a complete circulation in spring and autumn. During periods of stagnation a scarcity of oxygen occurs in the bottoms of the profundal. In spite of these similarities the conditions for the configuration of the fauna are different, mainly because of differing degrees of human interference. Taken as part of Lake Mälaren, L. Ullevifjärden has suffered little interference, whereas Ekoln has become the recipient through the River Fyrisån of, amongst other things, the sewage of the town of Uppsala. Furthermore, parts of the surroundings of Ekoln are densely settled and cultivated, while L. Ullevifjärden is almost completely surrounded by coniferous forest.

The differences between the two basins find expression in, e.g., the transparency of the water, which is higher in L. Ullevifjärden than in Ekoln. This is partly due to the fact that L. Ullevifjärden receives the precipitation of a limited area and is fed to a large extent by subsoil water. The most important feeder of Ekoln, the River Fyrisån, has a discharge of about 300 million cubicmetres per annum (Rep., Limnol. Inst. 1962).

The occurrence of higher aquatic vegetation is limited by stretches with steep shores. It is, however, most strongly developed in Ekoln. L. Ullevifjärden contains a rich submerged vegetation of, e.g., *Chara fragilis,* and a belt of free *Cladophora aegagropila* between the approximate depths of 5 and 12 metres. The sediment of the profundal consists of gyttja, which in L. Ullevifjärden contains lake ore.

In May 1964, as a part of the experimental activities of the Institute for Freshwater Research, Drottningholm, 5,000 yearlings of lake trout, *Salvelinus namaycush* WALBAUM, were implanted in L. Ullevifjärden.

2. Material and methods

For a number of years the lakes in question have been the object of excursions from the Institute of Zoology of the University of Uppsala. On these occasions the composition of the bottom fauna has been among the matters studied. Quantitative material was collected in L. Ullevifjärden in October 1959 and in Ekoln in May 1963. This material comprises 5,312 animals resulting from 21 samplings (bottom sampler: EKMAN-BIRGE). The samples were taken along lines stretching from the north-western shores of the lakes towards the deep portions. The samples were sifted with 0.6 gauge, and the weighing was carried out on material preserved in alcohol and with a tolerance of ±0.1 mg.

3. Results

Quantity. The bathymetric distribution of the bottom animals is shown in Table 1. An important difference between the two basins lies in the fact that in L. Ullevifjärden maximum abundance occurs in the littoral, while Ekoln exhibits a more abundant fauna in the region of the profundal.

The relatively low abundance in the uppermost littoral of L. Ullevifjärden may be due to the slight exposure of the shore. Fine sediments, but only in thin layers, occur, and are interrupted by blocks or gravelly regions. In the uppermost littoral of Ekoln the samples were taken in the offshore border of the belt of *Phragmites* in bottoms with organogenic sediments in different stages of decomposition.

In Ekoln the distribution by weight agrees on the whole with the distribution by individuals and emphasizes the differences between littoral and profundal in this lake and, at the same time, the differences from L. Ullevifjärden. The great weight within the 10-metre zone in Ekoln is, however, largely attributable to the occurrence of a specimen of *Viviparus viviparus* L., which by itself weighed about 11 grammes.

Table 1. The bathymetrical distribution of bottom animals in L. Ullevifjärden and Ekoln.

Depth. m	Number, ind./sq. m		Weight, grammes/sq. m	
	L. Ullevifj.	Ekoln	L. Ullevifj.	Ekoln
1	3,960	14,864	32.3 (93.1)	7.6
5	7,084	4,730	16.5	3.4 (255.3)
10	—	6,849	—	16.1
17	4,708	—	21.3	—
31	—	26,130	—	18.0
Total	5,390	13,143	22.9	11.3

Figures within brackets: incl. *Dreissensia polymorpha.*

Table 1 also shows the average abundance and biomass of animals for the entire material. The circumstance that in L. Ullevifjärden the average weight *per* individual is four times greater than in Ekoln is due to the differences in the qualitative composition of the fauna in the two lakes.

Quality. The fundamental difference between the faunas of the two lakes appears in Table 2.

The bottom fauna can be characterized as a crustacean fauna in L. Ullevifjärden and as an oligochaete fauna in Ekoln. In relation to these animal groups the share of the insects is limited in both lakes. Molluscs, too, are relatively few, although they are important with regard to weight.

From the point of view of abundance as well as weight the upper littoral of L. Ullevifjärden is dominated by insects and gastropods, the *Cladophora* carpet of the lower littoral by isopods, and the profundal by ampipods. In Ekoln the oligochaetes, mainly *Tubificidae,* occupy a dominant position

Table 2. The balance between the main groups of bottom animals in L. Ullevifjärden and Ekoln. In per cent.

	Number		Weight (excl. *Dreissensia*)	
	L. Ullevifj.	Ekoln	L. Ullevifj.	Ekoln
Insecta excl. *Chironom.*	10.4	2.6	7.6	3.8
Chironomidae	7.0	8.3	1.1	8.4
Amphipoda-Isopoda	61.6	0.5	61.7	1.4
Cladoc.+Copep.+Ostrac.	3.7	5.0	< 0.1	< 0.1
Gastropoda	4.3	0.7	26.6	28.0
Lamellibranchiata	2.0	0.7	0.4	1.7
Oligochaeta	10.2	74.1	1.9	53.2
Hirudinaea	0.6	0.4	0.7	2.7
Hydracarina	0.2	0.3	< 0.1	< 0.1
Nematoda	—	7.3	—	0.7
Hydrozoa	—	0.1	—	< 0.1
	100.0	100.0	100.0	100.0

in all depth zones. Their importance grows with increasing depth, their percentage of the total number of animals being 31 at 1 metre, 67 at 5 metres, 79 at 10 metres, and 99 at 31 metres.

Of the four important main groups of the fauna, the position of the insects, in particular depends upon the season having regard to the emergence in the summer. The chironomids are usually the most important group. In Ekoln they occur in an average density of 1,088 ind./m^2, and belong to a great extent to the main group *Chironomini,* including among other the group *Chironomus thummi-bathopilus.* The lack of exuviae upon the surface of the water and of swarming along the shores at the time of the sampling (May), together with the frequency of pupae in the material, indicates that at the time of the sampling emergence had not yet taken place in Ekoln. Investigations in lakes of southern Sweden point in the same direction; there the majority of the chironomids leave the bottoms in the period June—August (BRUNDIN 1949). In samples taken in Ekoln in October 1964 at a depth of 20 metres the chironomids constituted only 7 per cent of the fauna, while 88 per cent were oligochaetes.

In L. Ullevifjärden the major insect larvae are more numerous than the chironomids, which show an average abundance of 374 ind./m^2 and are represented mainly by species belonging to *Tanypodinae* and *Tanytarsini.* Even if it can be estimated that the majority of the chironomids of L. Ullevifjärden are represented in the bottoms in October (cf. BRUNDIN 1949), there nevertheless exists a possibility that part of the young populations has been lost in the sifting. A correction of the balance of the fauna in favour of the insects is therefore justified. Such a correction would probably not affect the characterization of the fauna as crustacean.

The remaining insects in L. Ullevifjärden are species of *Ephemerida, Trichoptera,* and *Coleoptera.* As examples we can mention *Ephemera vulgata* L., *Caenis moesta* BENGTS., *Centroptilum luteolum* MÜLL., *Molanna angustata* CURT., *Cyrnus* sp. and *Leptocerus* sp., and also *Deronectes depressus* FABR. and larvae of *Helmiini.* In Ekoln these big larvae are less numerous and restricted to the littoral, e.g. *Caenis horaria* L., *Cyrnus flavidus* Mc LACHL., and *Molanna angustata.* Towards greater depths we find *Chaoborus crystallinus* DE GEER and occasional ceratopogonids.

A very considerable proportion of the crustaceans in L. Ullevifjärden belongs to the marine-glacial relict forms *Pontoporeia affinis* LINDSTR., *Pallasea quadrispinosa* SARS and *Mesidothea entomon* L. In addition to these, *Asellus aquaticus* L. is of importance.

The major crustaceans occur in layers of different depths. *Mesidothea* is found only in the profundal and *Asellus* only in the littoral, where it is particulary numerous in the *Cladophora* carpet. Among the amphipods *Pallasea* has the greatest bathymetric amplitude for the season with the maximum development in the *Cladophora* carpet. *Pontoporeia* is most numerous

Table 3. Oligochaetes from L. Ullevifjärden and Ekoln. The material has been identified by Dr. R. O. BRINKHURST, University of Liverpool.

L. Ullevifj.	0.3 m, October	*Psammoryctes albicola* MICH. *Stylaria lacustris* L. *Limnodrilus udkemianus* CLAP. *Peloscolex ferox* EIS.
	17 m, October	*Tubifex tubifex* MÜLL. *Euilyodrilus haemmoniensis* MICH.
Ekoln	20 m, October	*Euilyodrilus haemmoniensis* MICH. *Aulodrilus pluriseta* PIGUET
	28 m, May	*Tubifex tubifex* MÜLL.

in the profundal, where it completely dominates the fauna. Among the crustaceans in layers near the bottom must also be reckoned *Mysis relicta* LOV., which occurs in qualitative samples from the lower littoral and the profundal.

In Ekoln only isolated specimens of these crustaceans have been obtained, viz. young individuals of *Pallasea* at 1 and 10 metres, *Pontoporeia* at 10 metres, and *Asellus* at a depth of 1 metre, *Mysis relicta,* which was observed by EKMAN (1907), has not been encountered (cf. GÖNCZI 1962).

The gastropod faunas are similar in the littoral of the two lakes. The following are common: *Limnæa peregra* MÜLL., *Bithynia tentaculata* L., *Gyraulus crista* L. and *G. albus* MÜLL., *Valvata macrostoma* STEENB., *V. cristata* MÜLL. and *V. piscinalis* MÜLL. In the littoral of Ekoln, in addition to the species above *Acroloxus lacustris* L. and *Viviparus viviparus* L. have been encountered. The occurrence of *Theoduxus fluviatilis* L. (about 80 ind./m^2) in the upper littoral of L. Ullevifjärden stresses the character of the sampling station of an exposed shore.

Among the oligochaetes the ecologically tolerant species *Tubifex tubifex* and *Euilyodrilus haemmoniensis* occur in the profundal of both basins (Table 3). According to BRINKHUST (personal communication) the absence of *Limnodrilus hoffmeisteri* in the material is remarkable. This species is otherwise common in most of the lakes investigated and is often established together with *T. tubifex, E. haemmoniensis* and *Aulodrilus pluriseta* (BRINKHURST 1964).

4. Discussion

It can be supposed that in recent times the fauna of Ekoln has suffered changes parallel with the increasing pollution of the water through human intervention. As an example we can mention that in 1907 EKMAN found 20 species of planktonic crustaceans in the lake. According to GÖNCZI only 5 species were found in 1962. Many indications suggest that originally the fauna of Ekoln agreed in many features with that of L. Ullevifjärden in our days. The two basins are situated within the same part of Lake Mälaren. Both basins started with eutrophic conditions with similar morphometric and climatological features.

The annual qualitative examinations of the fauna of L. Ullevifjärden and Ekoln exhibit good agreement with the results presented in this paper. For this reason the relatively limited quantitative material can be assumed to be roughly representative for the composition of the fauna in both lakes.

With respect to abundance, the littoral fauna of Ekoln does not seem to occupy an isolated position. For the month of July in the years 1940—41 PUKE (1948) reports for the littoral of Lake Mälaren an abundance of up to 10,500 ind./m^2 in the *Phragmites* belt. Abundances greater than that of the littoral of Ekoln are not unusual in eutrophic lakes (BRUNDIN 1949). The abundance in the profundal of Ekoln exceeds, on the other hand, the usual values in eutrophic lakes and points to conditions resulting from an increased eutrophy due to human agencies.

Within the littoral of Ekoln there occur species indicative of normal eutrophic conditions, e.g. in the gastropod and insect fauna. The divergences from L. Ullevifjärden are, however probably more obvious during winter, when the littoral of Ekoln does not receive a comparable addition of large relict forms within the *Crustacea*. But the most important factor for the assessment of the status of Ekoln is supplied by the dominant position of the oligochaetes in the whole basin and by its special conditions in the profundal.

Unfortunately only a few of the earlier examinations of the bottom fauna of Lake Mälaren have been published (ROSÉN 1915, ALM 1927, PUKE 1948). None of these investigations has provided a picture of the fauna that agrees with the one given here for L. Ullevifjärden and Ekoln. A universal feature to be noted is that the chironomids, especially the species of *Chironomus*, occupy a more dominant position in the fauna. For 1915—16 ALM reports the following relative distribution in the fauna of Lake Mälaren: *Chironomus* 36—56, *Oligochaeta* 26—48, and *Pontoporeia* 6—15 per cent of the entire fauna.

The most reliable basis for a further discussion is the comparison with ROSÉN's material collected in October 1913 in the profundal of Ekoln (Table 4).

Table 4. The relative abundance of some bottom animals in the profundal region (10—31 metres) of L. Ullevifjärden and Ekoln. In per cent.

	L. Ullevifj. 1959	Ekoln 1913	Ekoln 1963
Amphipoda	72	8	1
Chironomidae	9	70	3
Oligochaeta	15	21	95

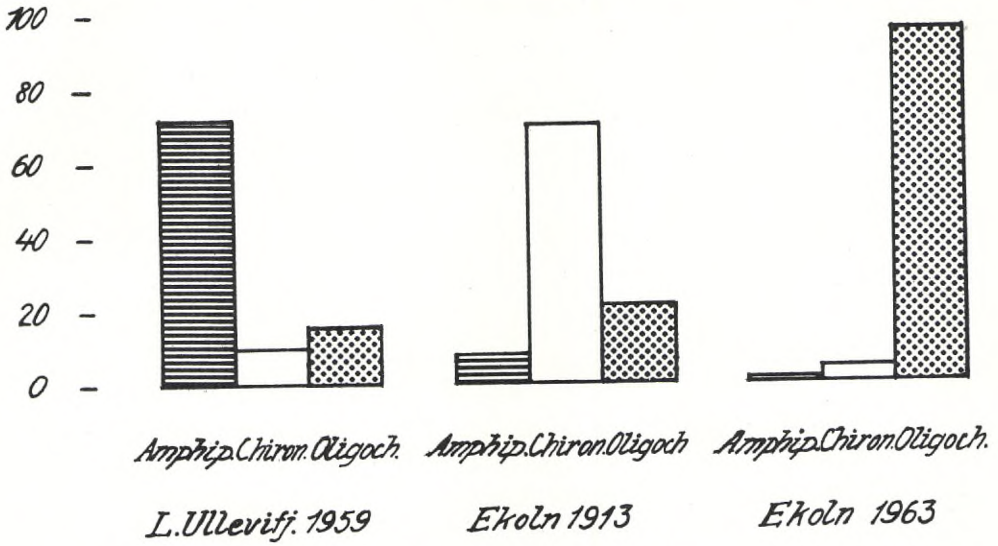


Fig. 1. The balance between the important groups of animals in the profundal of L. Ullevifjärden 1959, Ekoln 1913 and 1963. Expressed as percentage of the total number of individuals.

Rosén's results show that 50 years ago the fauna of the profundal in Ekoln was dominated by chironomids, that amphipods (*Pontoporeia*) occurred in a certain measure, and that the position of the oligochaetes was limited.

A comparison of the results of the different investigations suggests the conclusion that in Ekoln there has been a gradual development from a crustacean fauna first to a chironomid fauna and finally to an oligochaete fauna (Fig. 1).

Many circumstances support the assumption that the observed development within the bottom fauna usually accompanies increased eutrophy. Dominance of oligochaetes has, for instance, been established in the polluted Lake Växsjö, where according to BRUNDIN (1949) in October, 1943 the oligochaetes made up about 60 per cent of the entire fauna. In Hamburg the oligochaetes form up to 100 per cent of the fauna of the canals which are polluted by sewage (CASPERS and MANN 1961).

There seems to exist a certain relation between the exposure of the animals in the bottom and their degree of reaction. It appears that the big and mobile organisms in the bottom surface or in layers near the bottom are most sensitive to the worse conditions resulting from pollution. Among these organisms may be reckoned the marine-glacial relicts, but also numerous species, e.g. within the remaining crustaceans and insects of fair size. Worse conditions in the sediments seem to afflict mainly the insects, which seem to be

Table 5. The average abundance and biomass of the entire fauna and "fish food" organisms in L. Ullevifjärden and Ekoln.

	L. Ullevifj.	Ekoln	proportions
Entire fauna, ind./sq. m	5,400	13,100	1/2.5
"Fish food" ,, ...	4,500	1,600	3/1
Entire fauna, g/sq. m	22.9	11.3	2/1
"Fish food" ,, ...	22.2	4.7	5/1

more dependent upon the surface layers, meeting the water than are, e.g., the oligochaetes.

The degree of exposure in the bottoms also influences the relations between the animals and their predators. The above-outlined development from a fauna of crustaceans via one of insects towards an oligochaete fauna implies a gradually diminished availability of bottom organisms as food and, in connection with this, a simultaneous reduction in the utilization degree of bottom animals as fish food (cf. GRIMÅS 1963).

This connection between the exposition of the animals in the bottoms and their attitude towards different surrounding factors appears natural. Interference which submits the fauna to worsened environmental conditions has thus often the tendency of eliminating first of all exposed bottom organisms that are of importance from the point of view of production. By way of example we can mention the effect of the impoundment of lakes upon the qualitative composition of the bottom fauna (GRIMÅS 1965).

The qualitative composition of the bottom fauna thus gives indications about the position of the fauna in the production chain of the lake, and can in many cases be interpreted as indicative of the status of the lake. Of prime importance for the capacity of the lake for producing fish is, however, the actual quantity of available food organisms, expressed by abundance and biomass. A comparison in this respect between L. Ullevifjärden and Ekoln is given in Table 5.

If insects, gastropods, and the larger crustaceans are reckoned as the most important fish food organisms, then the average density of fish food in L. Ullevifjärden is thrice that in Ekoln in spite of the fact that the bottom fauna of Ekoln is twice as rich in animals. If the weight of the bottom organisms is taken into account, the difference between the two basins is still further enhanced.

The results of the investigation lead to the supposition that, in spite of a much lower standing crop of bottom animals, the potential production of fish is greater in L. Ullevifjärden than in Ekoln. They also stresses the importance of the qualitative composition of the bottom fauna in any discussion of the capacity of a water for the production of fish.

5. Summary

1. The bottom fauna has been studied in two basins of Lake Mälaren, viz. L. Ullevifjärden and Ekoln, which resemble each other morphometrically and climatologically but have undergone human interference to a different extent.
2. In L. Ullevifjärden maximum abundance is found within the littoral, and crustaceans, among them marine-glacial relicts, constitute an important element of the fauna. In Ekoln maximum abundance occurs within the profundal, and the bottom fauna is dominated by oligochaetes.
3. A comparison with earlier investigations in Ekoln suggests a gradual development of the bottom fauna from a crustacean fauna first to an insect fauna and then to an oligochaete fauna, this development proceeding in parallel with increasing pollution through human activity.
4. The connection between the exposure of the animals in the bottoms and their attitude towards different environmental factors is discussed.

6. References

ALM, G., 1927. Undersökningar över Mälarens bottenfauna. — *Medd. Kungl. Lantbr.st., nr 263,* 1—37. In Swedish.

BRINKHURST, R. O., 1964. Observations on the biology of lake-dwelling *Tubificidae.* — *Arch. Hydrobiol. 60,* 385—418.

BRUNDIN, L., 1949. Chironomiden und andere Bodentiere der südschwedischen Urgebirgseen. — *Rep. Inst. Freshw. Res., Drottningholm nr 30,* 1—914.

CASPERS, H., and MANN, H., 1961. Bodenfauna und Fischbestand in der Hamburger Alster. — *Abh. u. Verh. Naturwiss., Ver., Hamburg N.F. Bd. V,* 89—110.

EKMAN, S., 1907. Über das Crustaceenplankton des Ekoln (Mälaren) und über verschiedene Kategorien von marinen Relikten in schwedischen Binnenseen. — Zoologische Studien. Prof. Tullberg gewidmet. Upsala.

GÖNCZI, A., 1962. Undersökningar över Ekolns zooplankton och vattenkemi. — Limnologiska Institutionen, Uppsala. In Swedish. Mimeographed.

GRIMÅS, U., 1963. Reflections on the availability and utilization degree of bottom animals as fish food. — *Zool. Bidr. Upsala, 35,* 497—503.

— 1965. The short term effect of artificial water level fluctuations upon the littoral fauna of Lake Kultsjön, northern Sweden. — *Rep. Inst. Freshw. Res., Drottningholm, 46,* 5—21.

LIMN. INST., 1962. Fyrisån och dess biflöden. En recipientundersökning, — Upsala. In Swedish. Mimeographed.

LOHAMMAR, G., 1938. Wasserchemie und höhere Vegetation schwedischer Seen. — *Symb. botan. Upsaliensis, III: 1,* 1—252.

PUKE, C., 1948. Bottom fauna and environmental conditions in the littoral region of lakes. — *Rep. Inst. Freshw. Res., Drottningholm, 29,* 77—80.

ROSÉN, N., 1915. Redogörelse för bonitetsundersökningar i Mälaren och Boren. — *Medd. Kungl. Lantbr.st. nr 195, 29—40.* In Swedish.

Food segregation between salmonoid species in North Sweden

By NILS-ARVID NILSSON

This thesis is a summary of 9 papers published between the years 1955 and 1964. The different papers are referred to in the text by using roman numerals according to the following list.

I. 1955. Studies on the feeding habits of trout and char in North Swedish lakes. *Rept. Inst. Freshw. Res. Drottningholm 36:* 163—225.

II. 1957. On the feeding habits of trout in a stream of Northern Sweden. Ibid. *38:* 154—166.

III. 1958. On the food competition between two species of *Coregonus* in a North-Swedish lake. Ibid. *39:* 146—161.

IV. 1960. Seasonal fluctuations in the food segregation of trout, char and whitefish in 14 North-Swedish lakes. Ibid. *41:* 185—205.

V. 1961. The effect of water-level fluctuations on the feeding habits of trout and char in the Lakes Blåsjön and Jormsjön, North Sweden. Ibid. *42:* 238—261.

VI. 1962 a. With T. LINDSTRÖM. On the competition between whitefish species. In: *The Exploitation of Natural Animal Populations,* ed. LE CREN and HOLDGATE. Oxford.

VII. 1962 b. With U. GRIMÅS. Nahrungsfauna und Kanadische Seeforelle in Berner Gebirgsseen. *Schweiz. Z. Hydrologie XXIV* (1): 49—75.

VIII. 1963. Interaction between trout and char in Scandinavia. *Trans. Am. Fish. Soc. 92* (3): 276—285.

IX. 1964. Effects of impoundment on the feeding habits of brown trout and char in Lake Ransaren (Swedish Lappland). *Verh. Internat. Verein. Limnol. XV:* 444—452.

Some new material is added in Tables 1—7 and Figs. 1—3.

I. General survey of the problem

As is stated elsewhere in greater detail (I, VI, VIII) the present study is an attempt at demonstrating the situation that arises when two or more closely related species meet within the same area, especially with regard to their segregation into different niches. Thus it is in line with earlier works on food and habitat selection (cf. e.g. LACK 1947, SVÄRDSON 1949 a, GIBB 1954). SVÄRDSON (1949 a) pointed out in this context the connection between interspecific and intraspecific competition, stating that when interspecific competition is intense the species tends to be restricted to a narrow range, the "optimum" of the species, whereas during periods when intraspecific competition dominates, the species also spreads out over marginal, less favourable areas. BRIAN (1956) made an important distinction between "selective segregation" and "interactive segregation". Selective segregation means a definite difference in habitat and/or food selection due to the species in question being ecologically isolated in the sense expressed, for instance, in MAYR's (1951) species definition: "an aggregate of interbreeding natural populations which are not only reproductively isolated from other such aggregates but also ecologically specialized sufficiently *so as not to compete with other such species*".[1] Interactive segregation, on the other hand, means that interaction between the species forces them to magnify their differences in habitat or food selection. The interactive type of habitat segregation has for instance been demonstrated in fish as regards Atlantic salmon and trout (LINDROTH 1955, KALLEBERG 1958). The mechanism working in this case is interspecific fighting for territories. Interactive food segregation in fish was experimentally demonstrated by IVLEV (1961), who showed that the tendency of a species to prefer certain food items (as expressed by an "electivity index") changed in the presence of a competing species (op. cit. p.p. 224, 225).

Evidences for selective segregation in fish have for instance been given by FRYER (1959) in the case of the cichlids of Lake Nyasa. There is a need for comparative investigations on the frequency of interactive and selective segregation in the Arctic as compared to more tropical areas. The greater variation in the stomach contents in the Arctic pointed out e.g. by NIKOL'SKII (1962) might be reflected also in a high frequency of temporal overlap in food niches in this area, which also in general contains a "younger" fauna than the tropical ones. "Arctic and antarctic faunas are immature, still in the elementary stages of evolutionary 'learning'" (DUNBAR 1960).

The term of interspecific competition has been frequently used in the papers in question, mostly as an expression of an interaction between species populations that adversely affects natality, survival and/or individual growth in these populations (I, VI), which is a modification of the definition given by ODUM (1953). The author agrees with ANDREWARTHA and BIRCH (1954), LARKIN (1956) and others that the term competition should be avoided, if more exact descriptions of the interactions in question could be used. PARK's (1954) and BRIAN's (1956) subdivision of competition into the components of exploitation and interference has been especially useful in the present study (IV, VIII).

The importance of differential growth rate and resulting size distribution as a factor in ecological isolation has been stressed especially by SVÄRDSON (1949 b) when analyzing the systematics and ecology of the Scandinavian *Coregonus*-species, but it is interesting to note that this principle has also

---

[1] Author's italics.

been observed in primitive evertebrates such as the rotifers (genus *Polyarthra*) (PEJLER 1956).

It is obvious that the outmost complexity of the interactions within an ecosystem makes it very difficult to collect really significant data directly from nature. Very simple ecosystems with few species are in that connection to be favoured when trying to construct general models. The recently deglaciated circumpolar area is to be looked upon as such a favourable study object.

The present investigation was originally started with the aim of examining the changes in food habits resulting from the impoundments of the high mountain lakes of north Sweden. These lakes often contain just the two species of trout (*Salmo trutta* L.) and char (*Salvelinus alpinus* L.), in some cases also grayling (*Thymallus thymallus* L.), burbot (*Lota lota* L.) and minnow (*Phoxinus phoxinus* L.). The Norwegian experiences indicating that trout and char tend to compete when coexisting (DAHL 1920, SØMME 1933, AASS 1960) and the data obtained by experimental studies (SVÄRDSON 1949 c) and the study of the food habits of coexisting trout and char in the Swedish lakes called for the investigation of lakes inhabited by just one of the two species (I, VIII).

The economic importance of the whitefish (*Coregonus*) in the majority of lakes below the arctic-boreal trout-char-lakes in northern Sweden and the palearctic "*Coregonus*-problem" (SVÄRDSON 1957, 1958) also actualized a study of the feeding habits of three species of *Coregonus* (III, IV, VI).

The impoundment of some of the lakes in question which, above all, meant a considerable decrease in the available standing crop of bottom food (GRIMÅS 1961, 1965) gave an excellent opportunity to study what happens when food, tempting to several competing species, is removed. The investigation was carried out as a part of a joint effort between several persons and institutions (cf. e.g. SVÄRDSON 1957, LINDSTRÖM 1962, RODHE 1964, S. RUNNSTRÖM 1964, GRIMÅS 1965), which is one of the reasons why it could be restricted just to the problem of food segregation.

2. Material and methods

Test-fishing in remote areas are expensive operations, that in general can only be justified when more than one problem is to be studied. Most of the samples, consequently, have been taken in connection with test-fishing operations carried out for one or more reasons other than just studies of food habits. Above all, such lakes have been fished that were to be impounded or had already been impounded, and the material was mainly meant to support the submissions made to the Water Courts in connection with their treatment of matters of hydroelectric exploitation. The relatively small size of the material collected in lakes with allopatric populations of trout and char is one of the results of the abovementioned problem, besides that the number of such lakes is rather limited and they mostly are situated in very remote areas. In all, however, 21 lakes with allopatric trout and char, 14 lakes with sympatric trout and char, and 2 lakes with whitefish have been studied. The stomach contents of more than 6,000 trout and char and 2,000 whitefish have been analyzed.

To make the samples as equivalent as possible, there has during the whole time been an endeavour to make the test-fishing operations as similar as possible. As the fishing-technique developed, however, the methods were subject to some changes. Before 1950 the test-fishing thus was carried out with cotton nets, but after 1950 nylon nets were successively introduced. From 1953 on the composition of mesh sizes was also strictly standardized so that every gang of gill-nets consisted of the following nets and mesh sizes: 1 12r,[2] 1 16r, 2 18r, 2 20r, 2 24r, and 1 36r. In the cases long series of test-fishing were carried out, the fishing was restricted to fixed stations (V, IX).

The method adopted as regards the stomach samples was taken over from earlier collectors of material. This was made necessary by the urgency of comparing data from a long series of years. The method involves a simple volumetric measurement by means of displacement of fluid (I). For comparison other methods have been used concurrently, for instance counting and dominance noting. Remarkably little deviation between the data obtained by different methods has been observed. The author agrees with HYNES (1950) and others that rather simple methods could be used, at least if the investigation concerns problems of behaviour rather than production. The tendency observed in many species of fish to select their food so carefully that often just one type, or a large fraction of one type of food is found in each stomach strengthens this view. It also reduces the value of the often repeated argument that different food objects show different rate of digestion.

3. The feeding habits of allopatric trout and char

The food of allopatric trout and char has been summarized briefly in tables 1 and 2 (cf. also I: Figs. 21, 22 and Table 13, VIII: Figs. 3, 5). It is evident from the tables that the main food categories of char are large crustaceans (*Gammarus lacustris*) and molluscs, insect larvae and nymphs, (mostly *Trichoptera, Ephemeroptera* and *Chironomidae*) and insect imagines capsized at the surface of the water (mostly terrestrial ones). The latter category is especially marked in the case of Lake Korsvattnet which does not contain *Gammarus*. Just in one case has the consumption of *Cladocera* reached a level that makes one species a dominant food item (*Holopedium* in Skalvattnet, August 1960).

The food spectrum of the allopatric trout is very much the same, the main food categories being *Gammarus*, insect larvae (mostly *Trichoptera*) and

---

[2] r=rows per *aln* (1 *aln*=0.59 m).

terrestrial insects. It is remarkable that in three cases (Semningsjön, June and August 1962 and Parkajaure, August 1964) *Cladocera* (*Daphnia* and *Bythotrephes*) have been dominant food items.

As far as the material presented here allows a comparison between the food habit of allopatric trout and char, it may be stated that the similarities on the whole seem to be greater than the differences. Noteworthy is, however, an obvious preference for chironomid pupae in the case of char, for *Trichoptera* larvae in the case of trout. Char also, according to the present material, show tendencies towards cannibalism that is not at all discernible in the case of trout. This observation is supported by observations in fish hatcheries. It should, however, be borne in mind that allopatric trout, because of the juvenile fish being separated from the adults through habitat segregation, would have few opportunities for feeding on small fish.

A quite different view is obtained when taking into consideration the "dwarf char" of Korsvattnet (Table 1, I: Fig. 22 and Table 13), which is slow-growing with a small average size and on the whole feeding on *Cladocera*. This case brings us to the complicated and still unsolved problem of the occurrence of different species of char (cf. BERG 1948, MCPHAIL 1961). In the case of Korsvattnet the two types of char do not only have different diets, growth rates and breeding habits, but the "ordinary" fast-growing char to a great extent also prey on the "dwarf char".

4. The feeding habits of sympatric trout and char

Through a series of papers (I, IV, V, VIII) it has been pointed out that there is an obvious difference between the food of trout and char when the two species are coexisting. Tables 3 and 4, which are based on material from undisturbed lakes not previously published in connection with the discussion of the present problem, give further evidence for that view. A considerable temporal variation is, however, found. Although the author at present is not fully convinced of the validity of the discussion about the annual variations contained in paper no. I: p.p. 178—184, the fact still remains that such important variations exist.

The seasonal variations get especially interesting when taking into consideration the degree of segregation, as expressed by the percentage of overlap in food consumed (IV: Figs 1—5, 7). A high degree of similarity in feeding habits seems to exist when one type of food, e.g. through mass developments, is superabundant (IV: Fig. 8), or when the prey fauna as a whole has a maximum degree of availability, in this case in spring and early summer (GRIMÅS 1965).

A comparison between the food of allopatric and sympatric populations of trout and char gives further emphasis to these differences. The species displaying the greatest displacement in feeding ecology from the allopatric to the sympatric situation is the char that allopatrically eats bottom or surface food, sympatrically *Cladocera* and copepods. This change from bottom and surface food to *Cladocera* and copepods is mainly valid for small-sized char, but is also discernible for larger fish (VIII: Fig. 5, Tables 5 and 6). The maximum consumption of these small crustaceans does on the whole not coincide with their maximum abundance in the lakes (I, IV, cf. LINDSTRÖM 1952, AXELSON 1961, GRIMÅS 1961, LÖTMARKER 1964).

The removal of bottom food resulting from the impoundment of lakes in the Swedish high mountains (GRIMÅS 1965), causes obvious changes in feeding habits of both trout and char (V, VIII, IX). In principle it implies an increased consumption of *Cladocera* and copepods in the case of char, of winged insects in the case of trout. The disappearance of a continuous supply of available food in spring, pointed out by GRIMÅS (1961, 1965), should also result in an earlier segregation into different feeding niches in the impounded lakes. On the whole the removal of food results in increasingly restricted feeding niches during the whole season.

The food segregation is accompanied by a certain habitat segregation which mainly implies that trout are caught in shallow water close to the shore, while char are more pelagic (I: Fig. 14, V: Fig. 6). Recent experiments with the test fishing with floated gill nets has revealed that this fishing method in trout-char lakes primarily catches char (FAGERSTRÖM, GUSTAFSON and LINDSTRÖM 1962, RUNNSTRÖM 1964).

The feeding habits of juvenile fish have on the whole not been discussed in the papers in question, with the important exception of paper no. VI, where the problems of the ecology of juvenile fish was treated by LINDSTRÖM. In the case of trout and char the food of the young fish has little significance for the present problem simply because habitat segregation prevents individuals of the two species from contact with each other. It is true, however, that this may occur where char populations are found in running water (cf. CURRY-LINDAHL 1957) but such populations have still not been subjected to sampling.

Young trout in running water appear to consume large quantities of planktonic crustaceans carried out by the currents in the outflow of the lakes (II). In this context it may be worth mentioning that the size of the fish in all cases has appeared to be of great importance, principally implying plankton-feeding or feeding on small food objects in the case of small fish, larger food objects up to the size of prey fish in the case of large fish (I: Table 5, II: Fig. 4, III: Table 1, V: Tables 4, 5, 16 and 17, VI: Fig. 9, VII: Table 6, VIII: Fig. 5, IX: Fig. 3, 4, and 5.

5. The feeding habits of whitefish

The food segregation between different species of whitefish is in many ways similar to the trout-char relationships (III, IV, VI). The whitefish, however, are, as compared to trout and char, extremely closely related, which makes the basic pattern of their feeding ecology still more similar. Consequently the differential growth rate pointed out by SVÄRDSON (1949 b) might in this case be of great importance for keeping the species populations segregated.

The material presented in the present papers does not allow a close analysis of the mechanisms working in the segregation of whitefish. It is, however, known that there exists a rough correlation between the number of gillrakers and food (III). Of the three species investigated *C. peled* has moreover displayed a certain tendency towards a pelagic life with the feeding habits characterized by plankton (*Bosmina*) and surface food. The remarkable dual existence of *C. peled* as dwarfed plankton-eater in Vojmsjön and fast-growing insect-eater in Storavan—Uddjaur, where *C. lavaretus* has taken over the role of plankton-eater, has been interpreted as a result of, among other things, differences in the physical conditions of the two lake systems (VI). The fact, pointed out by NORLIN (1964), that the majority of the insects capsized at the surface of the water originate from the immediate surroundings, and the great "gathering capacity" of a complicated shoreline support the idea that Storavan—Uddjaur should contain a relatively large bulk of surface food, which in turn would favour *C. peled* as a surface-feeder.

6. Feeding behaviour

It might seem a truism to state that the feeding behaviour of the fish certainly is one of the key mechanisms working in food segregation. It should, however, be mentioned that there exists a complex of other factors that influence and facilitate food segregation. One is temperature that influences different species of fish in different ways, depending on their optima (cf. FRY 1948, GRAHAM 1949, GIBSON and FRY 1954). A second is an innate tendency towards diurnal or seasonal migration observed in many species of fish (cf. e.g. JOHNSON 1961, NORTHCOTE *et al.* 1964). A third is the swimbladder-function that is reflected in a differential ability for different species of fish to retain gas in the swimbladder when migrating from one depth to another (cf. TAIT 1960 and personal communication). Different species of fish also show different ability to react to changing concentrations of chemicals (e.g. CO_2) in water (HÖGLUND 1961). No significant difference between trout and char has, however, been recorded (op. cit. Fig. 36). Trout, in comparison with the *Salvelinus*-species is known to have rather high values for temperature sensitivity (optima and mortality). This makes trout more of a shallow-water fish than char, which is known to be able to migrate from great depths to the surface of the water in a short time. A sample of char, for instance, caught at the depth of 30 metres in Blåsjön appeared to have stomach contents mainly consisting of newly caught imagines of *Lycoridae*.

The mechanisms of food selection in fish have been carefully studied by IVLEV (1961). He showed, among other things, that food selection is influenced by hunger motivation, which principally finds expression in a tendency towards lesser selectivity during states of hunger. The density of the prey fauna and its degree of patchiness also influence the selectivity of the fish so that high density and high degree of "patchiness" cause the fish to select food more carefully than when the prey is rare or scattered.

On the whole every fish species has, judging from IVLEV's experiments, a "ranking list" of preferred and avoided food types. It was, however, possible to change the order of the "ranking list" by conditioning the fish to certain food types. IVLEV called this process of learning to prefer food that was not inherently preferred "trophic adaptation". In nature the obvious ability in fish to specialize on certain food types and rapidly, through learning, change to other types must be of great significance in the food segregation process (I, II, III, IV).

Fig. 1 illustrates an attempt at experimental testing of the reaction of fish (in this case *Salvelinus namaycush* WALB.) to a continuous change in the frequency of two food-types. One of them (liver cubes) appeared to be preferred before the other one (fish cubes). It is worth noting that the curves marking the consumption of food objects of the four experimental fish rise steeply as the frequency of the preferred food type increases, whereas the curves illustrating the consumption of the less preferred food rise more flatly. In other words the consumption curves for preferred food are inclined at the left, for less preferred food at the right. *Innate preference* is also indicated by the maximum consumption of the food occurring before the maximum frequency is arrived at. *Conditioned preference* on the other hand, is indicated by the maximum consumption of the less preferred food occurring after the maximum frequency has been passed. It is easy to imagine that, presuming the experimental model has a correspondence in nature, such slight differences in preference may tend to segregate individuals of different species when food is in limited supply, even if the differences basically are very small. The experiment also displays a certain individual variation. For instance, the fish "A", which was dominant, learned more quickly than the others to prefer liver cubes during the first 6 weeks when the experimental group was offered the two food types in equal frequency. This dominance reduced the opportunities for the other two fish to consume liver cubes. A similar limitation was displayed by the fish "D", which was introduced into the tank 10 weeks after the other fish. It appeared that this individual, which in the experimental records gave the impression of having consumed very little food, after some time had learned to pick up food objects from the bottom of the tank.

The difference in feeding behaviour between trout and char have been

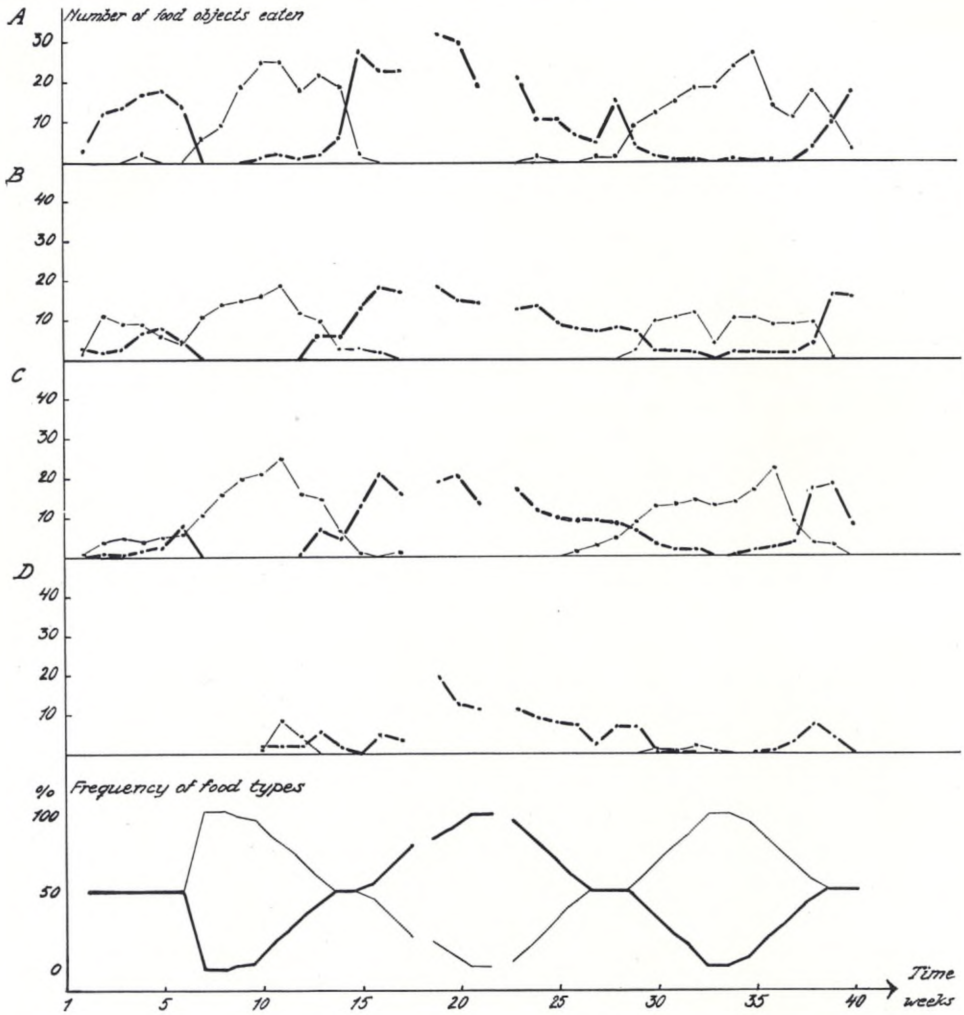


Fig. 1. The response of four lake trout (*Salvelinus namaycush*) to the offer of two types of food (liver cubes and fish cubes) occurring in fluctuating frequency. Coarse line=liver, thin line=fish. Every point represents the average daily consumption per week.

pointed out by Fabricius and Gustafson (1953) (cf. VIII). Juvenile trout and char kept in aquaria display very similar food preferences, although some tendencies towards differential food selection can be discerned, especially when the supply of food is limited (VIII: Fig. 6). An important difference between the two species is the territorial behaviour displayed by trout in contrast to the more pelagic char. The pelagic life of char does, however, not seem to imply a schooling behaviour *sensu strictu*, and aggressive behaviour ("nipping") has often been observed in captured groups (VIII, Table 7). It is interesting to note that the maximum frequency of interspecific aggres-

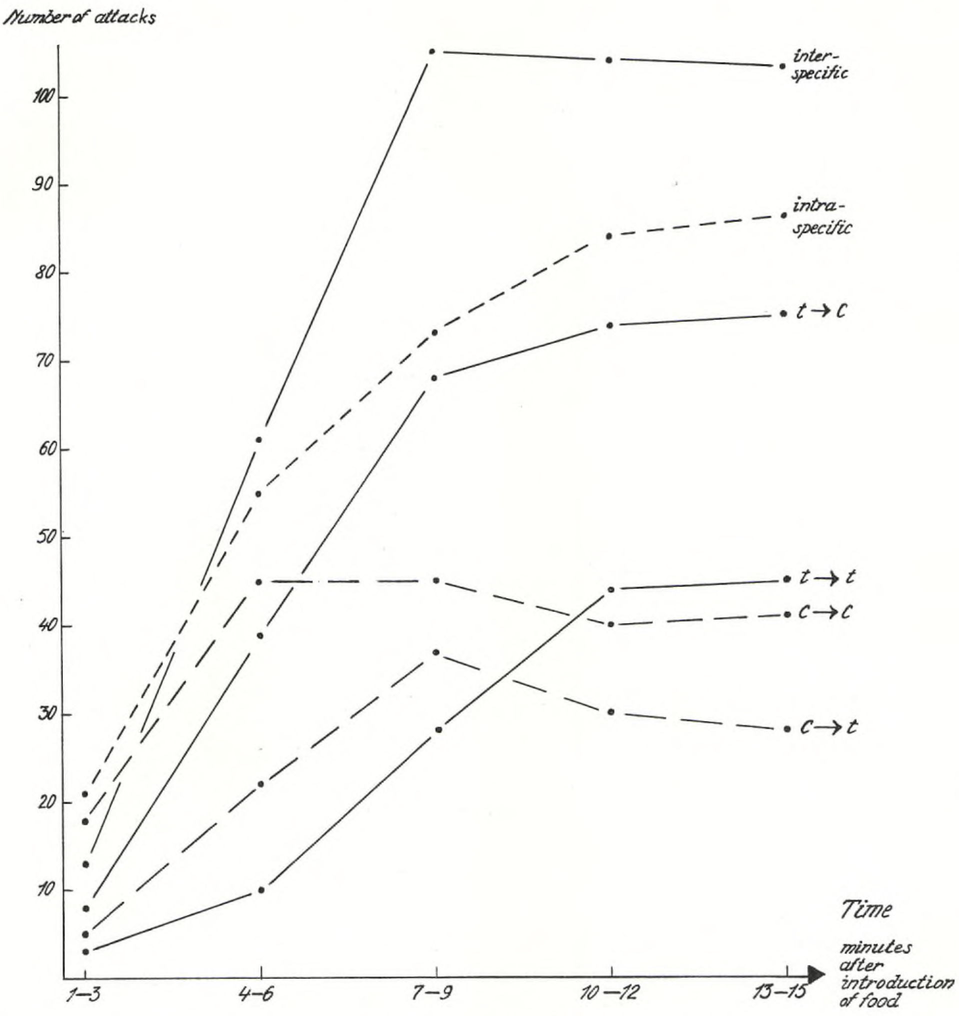


Fig. 2. Increasing aggressiveness in trout and char kept together in aquarium after food has been introduced. The diagram suggests a weakened aggressiveness in char after the trout having become dominant.

siveness has in all cases been observed in connection with feeding, being at a low rate just after an excess of food had been introduced but increasing as the food was getting limited (VIII: Fig. 6, Fig. 2). A tendency towards a decrease in the number of attacks per time unit when the experimental group has been forced to dwell in the same aquarium for a long time has also been observed (Fig. 3).

These observations are in agreement with what MACPHEE (1961) found in the case of coho salmon, *Oncorhynchus kisutch* (WALB.) and largemouth bass, *Micropterus salmoides* (LACÉPÈDE), KEENLEYSIDE and YAMAMOTO

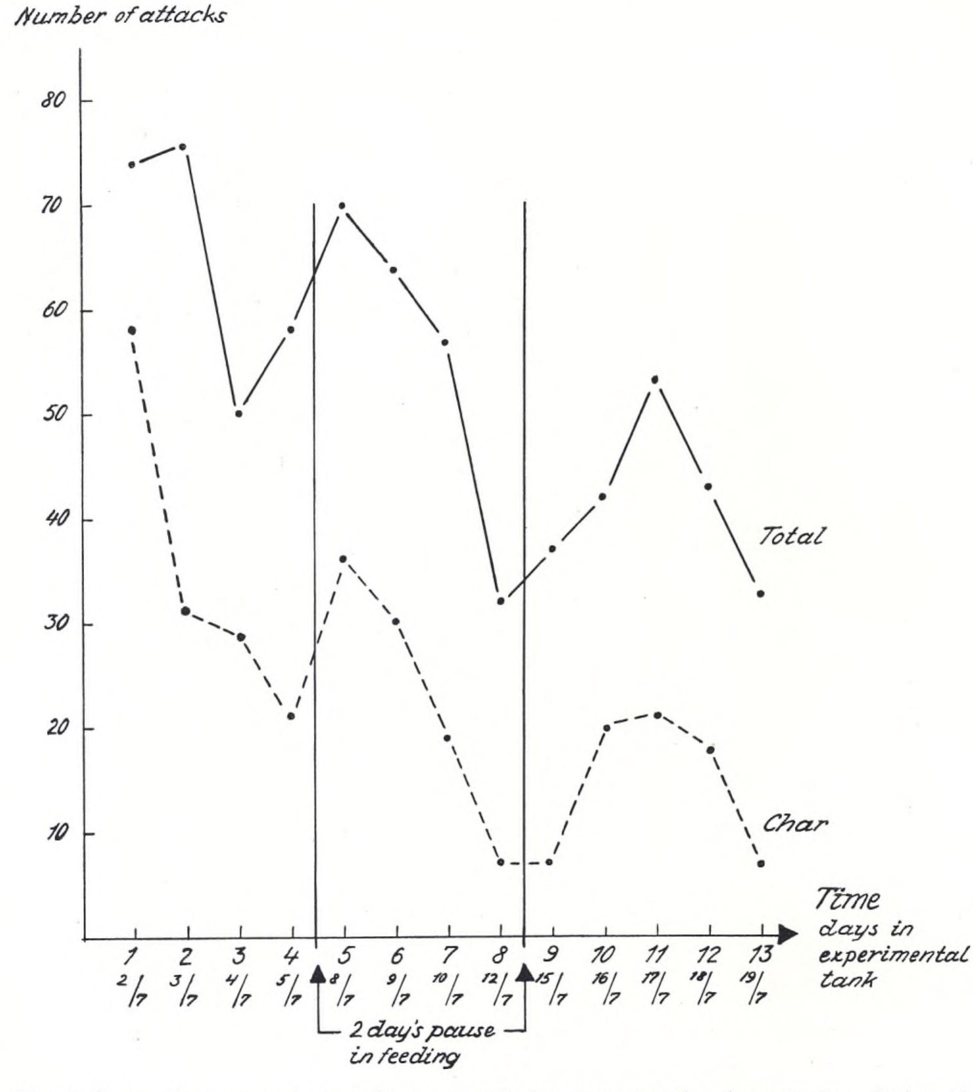


Fig. 3. Decreasing aggressiveness in trout and char kept together in aquarium during 18 days. The diagram suggests a temporal increase in aggressiveness after two days of hunger.

(1962) in the case of Atlantic salmon, and MAGNUSON (1962) in the case of medaka, *Oryzias latipes* (TEMMINCK and SCHLEGEL). MACPHEE also found that when food was first offered piece by piece, then dumped simultaneously on the water, dominant fish competed more strongly with subordinate fish than if the order was reversed, that is if the fish immediately got an excess of food. MAGNUSON stated that aggressive behaviour in the case of medaka is not a mechanism used in competition for space *per se*, but a mechanism which reserves a greater portion of a limited food supply. This seems according to the present experiments also be true for juvenile char.

7. Hypothesis

The material treated has presented the following phenomena as concerns the interrelationships of the salmonoid species examined:

1. Trout and char show considerable similarities in feeding habits when living in separate populations.

2. When coexisting in the same lake they are on the whole dissimilar, but a) they have similar feeding habits when food is in obvious superabundance and b) there is a tendency towards a more pronounced segregation when food is removed through the action of water-level fluctuations caused by hydroelectric exploitation.

3. The introduction of char into pure trout-lakes has resulted in changes in the trout populations, above all implying a decrease in the individual growth rate of the trout (cf. DAHL 1920, SØMME 1933, SCHMIDT-NIELSEN 1939, AASS 1960).

4. Similar food segregation has been observed in the case of three coexisting *Coregonus*-species.

The size of the material, showing among other things that the phenomena are repeated from case to case in spite of other circumstances being altered, and the basically unaltered fishing method, exclude the possibility of the phenomena being results of some sort of biased sampling.

The author has argued for the hypothesis that the observed phenomena are mainly results of interaction between the fish species in question (I, III, IV, VI, VIII), but this view does not exclude the action of other factors that are not directly bound to feeding ecology but contribute to the general view as it has hitherto developed. One important problem is the specific or racial conditions especially existing within the char complex. The fact that the allopatric char population in Skalvattnet (which is the one most carefully analyzed) was introduced from a trout-char lake, excludes the theory that all the investigated allopatric char populations consist of char species that are eliminated by trout when forced to compete with that species. It is in fact rather probable that a great many of the allopatric populations of trout and char in Scandinavia are results of early human actions of carrying fish of one species from lakes with mixed populations to empty lakes (cf. EKMAN 1910). There is in any case an urgent need for further analysis of the systematics and ecology of the different sub-populations of char.

The action of temperature does not seem to be an important factor in the cold subarctic lakes, where the surface water rarely reaches the peak of 12—15°C or more, and then just during a very short period in late summer (cf. AXELSON 1961, GRIMÅS 1961). It has also been found that trout and char often are caught at the same depths, even during periods of very marked food segregation (V: Fig. 6). The cold-stenothermal character of char and its ability to migrate from shallow water to great depths as well as a general pelagic character of behaviour, should, however, be helpful in keeping the species segregated when food is in limited supply.

The hypothesis adopted by the author is that the food segregation observed in sympatric populations of trout and char and different species of whitefish in North Swedish lakes is mainly a result of the exploitation of common resources and interference (IV, VI, VIII). Minute differences in food preference could be magnified during periods of short supply through a combined effect of innate preference and conditioning (Fig. 1); that is food slightly preferred by one species in relation to the other is "scrambled" away before the other species has learned to use it.

The general experience, that during experimental conditions there is a correlation between the degree of aggressiveness and supply of food in several species of fish, among others, juvenile trout and char (Table 5, Figs. 2 and 3), supports the theory that aggressiveness may also play a part in the segregation process. This does not necessarily presuppose a permanent aggressive behaviour, as subordinate fish should be able to learn the unpleasant nature of the dominants (cf. Fig. 3).

8. Fishery management implications

The general experience of the introduction of char into trout-lakes speaks in favour of the idea that the species combination, as far as arctic-boreal lakes are concerned, is unfavourable as growth rate is depressed by food competition. On the other hand, however, they at the same time share the resources in a way that relatively more organic production could be transformed into fish flesh. "Standing crop per acre increases as the number of species increases or as the niches are filled" (CARLANDER 1955). It should also be stressed in this connection that the general view arrived at by studying the interrelationships in the high mountain lakes treated here can not without further notice be applied to other types of lakes. For instance the south Swedish lakes have very different trophic standards, temperature conditions, and general faunistic compositions.

The effects of impoundments are in the long run adverse to the fish (S. RUNNSTRÖM 1964). Especially in the case of whitefish the resulting slowgrowing and smallsized fish are of little value for the fishermen. The idea has consequently arisen that a predator that better than trout could endure the changed conditions should be introduced in the ecosystem (SVÄRDSON 1956, VII). Studies of the food and growth of lake trout *(Salvelinus namaycush* WALBAUM) has indicated that this species might be suitable (VII), although Canadian experiences (CUERRIER 1954) show that it is not always the case.

Acknowledgements

I am deeply indebted to my teachers at the University of Uppsala, the late professor SVEN EKMAN, professors SVEN HÖRSTADIUS, KARL-GEORG NYHOLM, WILHELM RODHE and BERTIL KULLENBERG for their thorough training and continuous interest even after I had left the Zoological Institute for other work. The ideas that might be of value in this study are the results of the open and stimulating atmosphere at the Institute of Freshwater Research, Drottningholm, created by my colleagues, the late professors GUNNAR ALM and SVEN RUNNSTRÖM, Drs GUNNAR SVÄRDSON, THOROLF LINDSTRÖM, HARRY KALLEBERG and ULF GRIMÅS. The errors are mine.

References

AASS, P. 1960. Vassdragsreguleringene og fisket. Vedlegg till Årsberetningen om fiskeriundersökelser i regulerte vassdrag ved Inspektören for ferskvannsfiskets vitenskapelige avdelning. Mimeographed.

ANDREWARTHA, H. G. and L. C. BIRCH, 1954. *The Distribution and Abundance of Animals.* Chicago.

ARNEMO, R. 1959. Om förutsättningarna för fisken och fisket i några vatten vid Jofjället, Tärnaby. Limnological Institute, Uppsala. Typed manuscript.

AXELSON, J. 1961. Zooplankton and impoundment of two lakes in northern Sweden (Ransaren and Kultsjön). *Rept. Inst. Freshw. Res. Drottningholm 42:* 84—168.

BERG, L. S. 1948. *Les poissons des eaux douces de l'URSS et des pays limitrophes.* Vol. I. Leningrad.

BRIAN, M. V. 1956. Segregation of species of the ant genus *Myrmica. J. Anim. Ecol. 25:* 319—337.

CARLANDER, K. D. 1955. The standing crop of fish in lakes. *J. Fish. Res. Bd. Canada 12:* 543—570.

CUERRIER, J. P. 1954. The history of Lake Minnewanka with reference to the reactions of lake trout to artificial changes in environment. *Can. Fish. Cult. 15:* 1—9.

CURRY-LINDAHL, K. 1957. The occurrence of the char in running waters in arctic and highboreal areas in Sweden. *Kungl. Fysiogr. Sällsk. Lund Förh. 27* (12): 161—172.

DAHL, K. 1920. Studier over røje i ørretvand. *Norsk Jaeger- og Fiskeforb. Tidskr. 49.*

DUNBAR, M. J. 1960. The evolution of stability: Natural selection at the level of the ecosystem. In: *Evolution: Its Science and Doctrine.* Ed. T. W. M. CAMERON. Toronto.

EKMAN, S. 1910. Om människans andel i fiskfaunans spridning till det inre Norrlands vatten. *Ymer 30:* 133—140.

FABRICIUS, E., K. J. GUSTAFSON. 1954. Further aquarium observations on the spawning behaviour of the char, *Salmo alpinus* L. *Rept. Inst. Freshw. Res. Drottningholm 35:* 58—104.

FAGERSTRÖM, Å., K. J. GUSTAFSON, T. LINDSTRÖM. 1962. Under ytan — Fiskräkning och individtillväxt i ett fjällvatten. *Svenskt Fiske 7:* 246—250.

FRY, F. E. J. 1948. Temperature relations of salmonoids. *Proc Canad. Comm. Freshw. Fish.* Res. 1 Meet.

FRYER, G. 1959. Some aspects of evolution in Lake Nyasa. *Evolution XIII* (4): 440—451.

GIBB, J. 1954. Feeding ecology of tits, with notes on tree-creeper and goldcrest. *Ibis 96:* 513—543.

GIBSON, E. S. and F. E. J. FRY. 1954. The performance of the lake trout, *Salvelinus namaycush,* at various levels of temperature and oxygen pressure. *Can. J. Zool. 32:* 252—260.

GRAHAM, J. M. 1949. Some effects of temperature and oxygen pressure on the metabolism and activity of the speckled trout, *Salvelinus fontinalis. Can. J. Zool. 27:* 270—288.

GRIMÅS, U. 1961. The bottom fauna of natural and impounded lakes in northern Sweden (Ankarvattnet and Blåsjön). *Rept. Inst. Freshw. Res. Drottningholm 42:* 183—237.

— 1965. *Effects of impoundment on the bottom fauna of high mountain lakes.* Thesis. Uppsala.

HYNES, H. B. N. 1950. The food of freshwater sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*) with a review of methods used in studies of the food of fishes. *J. Anim. Ecol. 19:* 36—58.

HÖGLUND, L. B. 1961. The reactions of fish in concentration gradients. *Rept. Inst. Freshw. Res. Drottningholm 43:* 1—147.

IVLEV, V. S. 1961. *Experimental Ecology of the Feeding of Fishes.* New Haven. Russian original published 1955.

JOHNSON, W. E. 1961. Aspects of the theory of a pelagic, zooplankton-eating fish. *Verh. Internat. Verein. Limnol. 14:* 727—731.

KALLEBERG, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *S. trutta* L.). *Rept. Inst. Freshw. Res. Drottningholm 39:* 55—98.

KEENLEYSIDE, M. H. A., F. T. YAMAMOTO. 1962. Territorial behaviour of juvenile atlantic salmon (*Salmo salar* L.). *Behaviour XIX* (1—2): 139—169.

LACK, D. 1947. *Darwin's Finches.* Cambridge.

LARKIN, P. A. 1956. Interspecific competition and population control in freshwater fish. *J. Fish. Res. Bd. Canada 13:* 327—342.

LINDROTH, A. 1955. Distribution, territorial behaviour and movements of sea trout fry in the River Indalsälven. *Rept. Inst. Freshw. Res. Drottningholm 36:* 104—119.

LINDSTRÖM, T. 1952. Sur l'ecologie du zooplankton Crustacé. *Rept. Inst. Freshw. Res. Drottningholm 33:* 70—165.

— 1962. Life history of whitefish young in two lake reservoirs. *Rept. Inst. Freshw. Res. Drottningholm 43:* 113—144.

LÖTMARKER, T. 1964. Studies on planktonic Crustacea in thirteen lakes in northern Sweden. *Rept. Inst. Freshw. Res. Drottningholm 45:* 113—176.

MACPHEE, C. 1961. An experimental study of competition for food in fish. *Ecology. 42* (4): 666—681.

MCPHAIL, J. D. 1961. A systematic study of the *Salvelinus alpinus* complex in North America. *J. Fish. Res. Bd. Can. 18* (5): 793—816.

MAGNUSON, J. J. 1962. An analysis of aggressive behaviour, growth, and competition for food and space in medaka (*Oryzias latipes* (*Pisces, Cyprinodontidae*). *Can. J. Zool. 40:* 313—363.

MAYR, E. 1951. Speciation in birds. Progress report on the years 1938—1950. *Proc. Xth Int. Ornith. Congr. 1950.* Uppsala.

NIKOL'SKII, G. V. 1962. Discussion p. 340 in *The Exploitation of Natural Animal Populations,* ed. LECREN and HOLDGATE. Oxford.

NORLIN, Å. 1964. The occurrence of terrestrial insects on the surface of two lakes in northern Sweden (Ankarvattnet and Blåsjön). *Rept. Inst. Freshw. Res. Drottningholm 45:* 196—205.

NORTHCOTE, T. G., H. W. LORZ, J. C. MAC LEOD. 1964. Studies on diel vertical movement of fishes in a British Columbia lake. *Verh. Internat. Verein. Limnol. XV:* 940—946.

ODUM, E. P. 1953. *Fundamentals of Ecology.* Philadelphia.

PARK, T. 1954. Experimental studies of interspecies competition II. *Physiol. Zoöl. 27:* 177—238.

PEJLER, B. 1956. Introgression in planktonic Rotatoria with some points of view on its causes and conceivable results. *Evolution X* (3) : 246—261.

RODHE, W. 1964. Effects of impoundment on water chemistry and plankton in Lake Ransaren (Swedish Lappland). *Verh. Internat. Verein. Limnol. XV:* 437—443.

RUNNSTRÖM, H. 1964. Fiskeredskapsförsök. *Vattenkraft-Fiske* nr 6. Mimeographed.

RUNNSTRÖM, S. 1964. Effects of impoundment on the growth of *Salmo trutta* and *Salvelinus alpinus* in Lake Ransaren (Swedish Lappland). *Verh. Internat. Limnol. XV:* 453—461.

SCHMIDT-NIELSEN, K. 1939. Comparative studies on the food competition between trout and the char. *Det Kgl. Norske Vidensk. Selsk. Skr. 4*: 1—45.

SVÄRDSON, G. 1949 a. Competition and habitat selection in birds. *Oikos 1:* 157—174.

— 1949 b. The coregonid problem. Some general aspects of the problem. *Rept. Inst. Freshw. Res. Drottningholm 29:* 89—101.

— 1949 c. Competition between trout and char (*Salmo trutta* and *S. alpinus*). *Rept. Inst. Freshw. Res. Drottningholm 29:* 108—111.

— 1956. Experiment med fiskevatten. *Svensk Fiskeri Tidskr. 11:* 158—161, 12: 171—177.

— 1957. The coregonid problem VI. The palearctic species and their intergrades. *Rept. Inst. Freshw. Res. Drottningholm 38:* 267—356.

SØMME, S. 1933. Undersøkelser over maveindhold av røie (*Salmo alpinus* L.). *Nyt Mag. for Naturvidensk. B. LXXIII:* 115—136.

TAIT, J. S. 1960. The first filling of the swim bladder in salmonoids. *Can. J. Zool. 38:* 179—187.

Table 1. Food of allopatric char. Mean percentage of stomach volume.

	Fish	Cladocera & Copepoda	Large crustaceans & molluscs	Insect larvae & nymphs	Insect imagines "surface food"	Miscellaneous	Number of stomachs
Skalvattnet							
July 1960	—	3.1	8.9	*58.3*	28.4	1.3	112
August	0.8	22.0	23.5	*27.8*	20.7	5.2	107
October 1960	0.5	3.8	*56.7*	31.5	0.4	7.1	146
Korsvattnet							
July 1943	5.0	7.3	2.7	36.8	*45.5*	2.7	30
July 1944	3.5	21.2	—	*65.2*	10.0	—	17
September 1944 ..	16.0	—	7.0	*54.0*	23.0	—	10
July 1945	—	9.0	0.3	*72.5*	18.2	—	31
July 1947	4.5	13.1	—	17.7	*64.7*	—	44
"Dwarf char"							
July 1944	—	*71.5*	—	19.6	7.8	1.1	21
September 1944 ..	—	41.8	4.4	*44.2*	4.8	4.8	24
Övre Oldsjön							
July 1945	—	15.5	0.9	*66.3*	16.7	0.7	39
July 1947	—	19.4	3.6	*67.5*	8.9	0.6	29
Virihaure							
July 1964	4.5	1.1	1.2	*85.2*	4.4	3.7	88
Allesjaure							
August 1963	—	22.5	*65.9*	8.8	2.2	0.5	75
Jofjället 3[1]							
August 1958	—	—	15.1	*72.5*	11.5	0.9	22
Jofjället 4[1]							
August 1958	—	8.5	8.9	*77.6*	2.8	2.2	23
Tarraure[2]							
August 1964	0.1	9.6	40.0	*45.1*	1.5	3.7	74

[1] ARNEMO (1950).

[2] Material kindly placed at disposal by Mr. THORBJÖRN SJÖSTRÖM.

Table 2. Food of allopatric trout.

	Fish	Cladocera	Large crustaceans & molluscs	Insect larvae & nymphs	Insect imagines "surface food"	Miscellaneous	Number of stomachs
Abelvattnet							
July 1960	—	4.7	30.1	*57.5*	7.0	0.6	23
August 1960	—	17.6	*38.0*	20.5	23.4	0.5	95
Semningsjön							
July 1946	—	—	15.3	*49.0*	35.0	0.7	10
August 1946	—	12.6	9.9	*40.5*	37.1	—	15
June 1962	—	26.5	33.9	*39.3*	0.3	—	15
July 1962	—	5.3	34.5	*45.7*	14.1	0.4	18
August 1962	—	*54.8*	10.7	30.8	1.7	2.0	41
September 1962	—	22.6	25.1	*43.8*	6.8	1.8	85
Parkajaure[1]							
August 1964	—	*90.9*	4.3	1.1	—	3.7	51
Unna Parkajaure							
August 1964	—	29.8	18.7	*41.0*	5.0	5.5	15
Tåresjaure							
August 1964	—	10.1	*62.1*	25.1	2.6	—	21
Piädnak							
August 1964	—	33.1	21.9	*42.3*	2.6	—	8
Lastak a							
September 1964	—	5.4	*44.7*	5.9	37.9	6.1	29
Lastak b							
September 1964	—	—	*41.7*	—	41.7	16.7	24
Lastak g							
September 1964	—	—	*44.5*	0.9	42.1	12.5	27
Lastak k							
September 1964	—	—	*89.0*	—	11.0	—	6
Vuoka a							
September 1964	—	8.4	*74.4*	0.6	1.4	15.3	25
Vuoka b							
September 1964	—	—	*73.6*	1.4	1.2	23.8	29
Rovejaure							
July 1964	—	—	18.3	*81.7*	—	—	16

[1] Material from 1964 kindly placed at disposal by Mr. Thorbjörn Sjöström.

Table 3. Food of sympatric char.

	Fish	Cladocera & Copepoda	Large crustaceans & molluscs	Insect larvae & nymphs	Insect imagines "surface food"	Miscellaneous	Number of stomachs
Jormsjön							
July 1944	—	*44.9*	26.8	21.6	6.6	0.1	55
August 1945	3.3	*52.6*	42.9	0.8	0.2	0.2	30
October 1945 ..	—	41.5	13.3	—	—	*45.2* [1]	43
August 1946	—	*70.1*	2.6	14.0	13.3	—	30
September 1946	—	*79.8*	1.2	—	1.2	17.8	108
Ankarvattnet							
July—Aug. 1959	—	*48.4*	41.5	10.1	—	—	24
Sept.—Nov. 1959	—	*55.9*	41.9	2.2	—	—	52
Kultsjön							
July 1958	—	*60.8*	—	20.9	16.9	1.4	25
August 1958	—	*79.2*	0.2	14.1	6.1	0.3	25
September 1958 ..	—	*83.3*	12.7	3.4	0.7	—	25
October 1958 ..	—	*80.0*	10.0	9.7	0.5	—	24
Ransaren							
July 1954	—	23.0	13.7	*45.7*	17.1	0.5	45
August 1954	0.3	*48.5*	25.4	16.1	7.7	2.0	90
September 1954	3.5	*63.3*	18.8	2.7	11.2	0.5	57
October 1954 ...	—	40.6	*45.1*	10.8	3.3	0.2	69

---

[1] Eggs of char.

Table 4. Food of sympatric trout.

	Fish	Cladocera	Large crustaceans & molluscs	Insect larvae & nymphs	Insect imagines "surface food"	Miscellaneous	Number of stomachs
Jormsjön							
July 1944	—	—	29.9	*48.7*	21.4	—	49
August 1945 ..	5.6	24.2	*65.3*	4.9	—	—	41
August 1946 ..	—	9.6	29.1	*42.2*	18.6	0.5	59
Ankarvattnet							
July—Aug. 1959	—	5.8	*62.7*	14.0	17.5	—	52
Sept.—Nov. 1959	—	3.8	*40.3*	37.8	17.4	0.7	41
Kultsjön							
July 1958	0.9	—	0.8	*60.3*	26.7	11.1	9
August 1958	0.2	—	6.8	*60.2*	32.9	—	6
September 1958	16.0	15.0	6.5	*48.4*	14.1	—	7
Ransaren							
July 1954	4.0	—	10.8	20.3	*64.6*	0.3	71
August 1954	3.9	1.9	11.7	28.1	*54.2*	0.1	88
September 1954	—	1.7	25.3	*43.9*	27.3	1.8	15
October 1954	7.6	0.2	13.8	*60.8*	15.8	1.8	71

Table 5. The food of char of different size-classes in Lake Tarraure, August 1964. Mean percentage of stomach volume.

	Size class			
	2 151—200 mm	3 201—300 mm	4 301—400 mm	5 > 400 mm
Fish	—	0.5	—	—
Eurycercus	14.2	12.2	6.0	—
Lepidurus	—	—	1.4	—
Gammarus	31.6	18.0	37.9	64.3
Lymnaea	7.8	8.2	4.6	—
Sphaeriidae	—	6.7	—	—
Pulmonata	—	—	2.2	—
Chironomidae l.	0.3	—	—	—
Dytiscidae l.	1.6	—	—	—
Ephemeroptera l.	16.8	12.5	3.9	33.8
Tipulidae l.	—	—	0.9	—
Trichoptera l. ...	11.9	2.4	7.4	—
Chironomidae p.	1.6	24.7	17.9	0.5
Trichoptera p. ..	6.2	9.7	8.4	1.4
Trichoptera i. ..	1.3	—	0.1	—
Terr. insects	5.0	—	7.2	—
Miscellaneous ..	1.7	5.1	2.1	—

Table 6. The food of char of different size-classes in Lake Virihaure, July 1964.

	Size class			
	2 151—200 mm	3 201—300 mm	4 301—400 mm	5 > 400 mm
Fish	—	4.2	—	100
Daphnia	—	—	1.3	—
Eurycercus	6.7	—	—	—
Gammarus	13.3	0.4	—	—
Lymnaea	—	—	0.9	—
Chironomidae l.	10.6	26.9	21.5	—
Simuliidae l.	—	2.2	5.3	—
Tipulidae l.	—	—	0.9	—
Ephemeroptera l.	—	0.1	2.9	—
Plecoptera l.	—	0.2	0.2	—
Trichoptera l.	—	0.4	2.2	—
Chironomidae p.	69.4	51.8	57.7	—
Trichoptera p.	—	—	1.0	—
Chironomidae i.	—	0.1	—	—
Tipulidae i.	—	—	0.1	—
Coleoptera i.	—	1.4	0.2	—
Plecoptera i.	—	—	0.1	—
Trichoptera i.	—	—	0.1	—
Terr. insects	—	4.6	3.1	—
Miscellaneous	—	7.7	2.5	—

Table 7. Number of intraspecific and interspecific attacks in an aquarium containing 10 juvenile trout (t) and char (c) counted during 15 minutes after food has been introduced (observation time=16 days).

Day	Number of trout (t) and char (c)		Minutes after the introduction of food																				Sum
			1—3				4—6				7—9				10—12				13—15				
	t	c	t-t	c-c	t-c	c-t	t-t	c-c	t-c	c-t	t-t	c-c	t-c	c-t	t-t	c-c	t-c	c-t	t-t	c-c	t-c	c-t	
1	10	10	—	3	—	1	—	6	1	5	—	6	5	5	2	9	2	5	2	11	4	7	74
2	10	10	—	3	1	—	2	5	5	2	—	4	13	3	5	2	7	6	2	4	10	2	76
3	10	10	—	1	—	—	—	4	1	1	1	4	4	6	2	4	6	2	2	5	5	2	50
4	10	10	—	1	—	1	—	—	1	2	2	4	4	6	6	2	8	3	4	—	12	2	58
5	10	10	—	1	—	—	1	6	2	6	2	5	4	4	2	5	8	2	7	3	8	4	70
6	10	10	1	1	—	—	—	7	3	3	4	6	6	2	2	1	8	4	6	6	4	—	64
7	10	10	1	2	1	2	1	2	1	—	2	4	6	1	5	3	11	—	5	2	5	3	57
8	10	10	—	—	1	—	—	—	3	—	4	2	4	—	5	3	4	—	2	2	2	—	32
9	10	10	1	—	3	1	3	—	8	—	6	3	1	—	1	1	1	2	3	—	3	—	37
10	10	10	—	1	1	—	—	4	1	1	2	1	4	4	2	1	5	3	1	—	6	5	42
11	10	10	—	1	—	—	2	2	4	—	1	3	6	4	4	3	6	3	2	3	7	2	53
12	10	10	—	4	1	—	1	5	5	1	1	2	5	1	2	2	3	—	3	2	4	1	43
13	10	10	—	—	—	—	—	4	4	—	2	1	5	1	4	—	4	—	4	1	3	—	33
14	8	10	—	—	—	—	—	—	—	—	—	—	—	—	2	4	1	—	2	2	2	—	13
15	7	10	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1
16	7	10	—	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	2
	Sum		3	18	8	5	10	45	39	22	28	45	68	37	44	40	74	30	45	41	75	28	
			21		13		55		61		73		105		84		104		86		103		

Experiments on the transplantation of *Mysis relicta* LOVÉN into Swedish lakes

By MAGNUS FÜRST

Contents

1. Introduction

The background to the present attempts to transplant *Mysis relicta* is the extensive exploitation of the Swedish inland waters for hydro-electric purposes and the effect of this on the freshwater ecosystems. The influence of lake impoundment upon the bottom fauna in Northern Swedish lakes has been studied by GRIMÅS (1961). He established a quantitative reduction of the bottom fauna, especially within the annual amplitude of the water level. A qualitative change appears simultaneously — this, too, being to the disadvantage of the fish. After the impoundment, species that are less available and less valuable as fish food constitute the greater part of the biomass (literature reviewed by AASS 1958, LINDSTRÖM 1962, NILSSON 1964, RODHE 1964, RUNNSTRÖM 1964, GRIMÅS 1965). Since most impounded lakes are situated above the highest postglacial shoreline it is natural that the need for new food organisms should be supplied by the introduction of glacial-relict crustaceans, especially *Mysis relicta, Pallasea quadrispinosa* SARS and *Gammaracanthus lacustris* SARS (cf. e.g. EKMAN 1920, HOLMQUIST 1959, SEGERSTRÅLE 1957, 1962).

The importance of introducing suitable evertebrates as fish food organisms in freshwater has earlier been pointed out by DAHL 1915, HUITFELDT-KAAS 1916, SÖMME 1936, MATHISEN 1953 in Norway, by CLEMENTS et. al. 1939, LARKIN 1951, 1952 in Canada and by a great many authors in the Soviet Union, among others UZVA 1936, KARPEVIC 1948, 1960, 1962, GERD 1954, GORDJEJEV 1954, MARKOVSKIJ 1954, GRESE 1955, PIROSCHNIKOW 1955, KRUGLOVA 1957, ZURAVEL 1958, JOFFE 1958.

The only known instance of a successful introduction of *Mysis relicta* is

Table 1. Transplantations effected up to the end of 1961 by the Institute of Freshwater Research. The transplantations of 1954 were led by K. J. GUSTAFSON, 1957 by K.-J. GUSTAFSON and H. LÖFFLER, 1959 by N.-A. NILSSON and S. DAHLQUIST, 1960, 1961, 1964 by M. FÜRST.

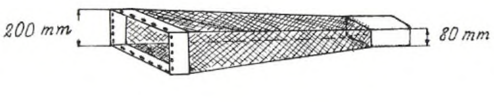
Year	From Lake	To Lake	Species	Number
1954	Mälaren	Storsjön (Härjedalen)	*Mysis relicta*	200
1957	Vättern	Torrön	*Mysis relicta*	20 000
1959	»	Anjan	*Mysis relicta*	20—30 000
»	»	»	*Pallasea quadrispinosa*	A few thousands of each
»	»	»	*Gammaracanthus lacustris*	
1960	»	»	*Mysis relicta*	25 000
»	»	»	*Pallasea*	2 000
»	»	»	*Gammaracanthus*	
»	»	Lillrönningen in Kall	*Mysis relicta*	2 000
»	»	» » »	*Pallasea*	200
»	»	» » »	*Gammaracanthus*	
1961	Mälaren	Kvarnbergsvattnet	*Limnocalanus macrurus*	5 mill.
»	»	Tarn at Skalstugan (0.25 ha)	*Mysis relicta*	1 000
»	Vättern	Anjan	*Mysis relicta*	0.5 mill
»	»	»	*Pallasea*	5—8 000
»	»	»	*Gammaracanthus*	
»	Mälaren	Lill-Tannsjön, Sollefteå (100 ha)	*Mysis relicta*	25 000

that from Kootenay Lake in British Columbia (SPARROW et al. 1964). RICKER (1959) has published other attempts at transplantation made in Canada. LINN and FRANTZ (1965) recently described an attempt at introducing *Mysis relicta* into four lakes in California and Nevada. In the U.S.S.R. *Mysis relicta, Pallasea quadrispinosa* and *Pontoporeia affinis* have been transplanted several times, but successes have been mentioned only in the case of other freshwater evertebrates, especially some Ponto-Kaspian mysides. The first introduction of *Mysis relicta* in Sweden was made by K. J. GUSTAFSON 1954. Subsequently the following persons have taken part in the work in addition to the author: N.-A. NILSSON, S. DAHLQUIST, A. GAD, O. HURTIG, B. IDESTRÖM, P.-O. JONSON and A. KLITGAARD.

2. Transplantations effected up to the end of 1961 and aquarium experiments

The Institute of Freshwater Research, beginning in 1954, has made the following attempts to introduce new fish-food organisms (Table 1). In Lake Vättern the animals were always collected in filterbasins used for the purification of the lake water for municipal purposes. Especially during winter the catches were good and before the trawl was constructed this was the only practicable way of procuring enough animals.

After 0.5 million *Mysis relicta* had been transported 900 km by lorry to Lake Anjan in 1961, a survival check was made. All the animals were found



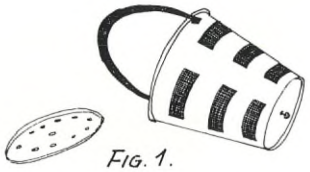


FIG. 1.

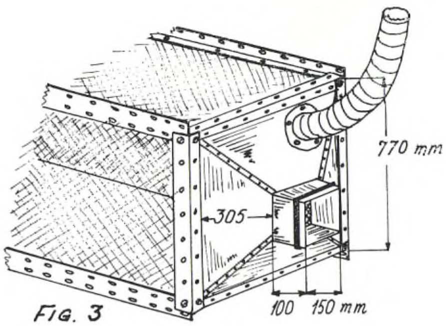
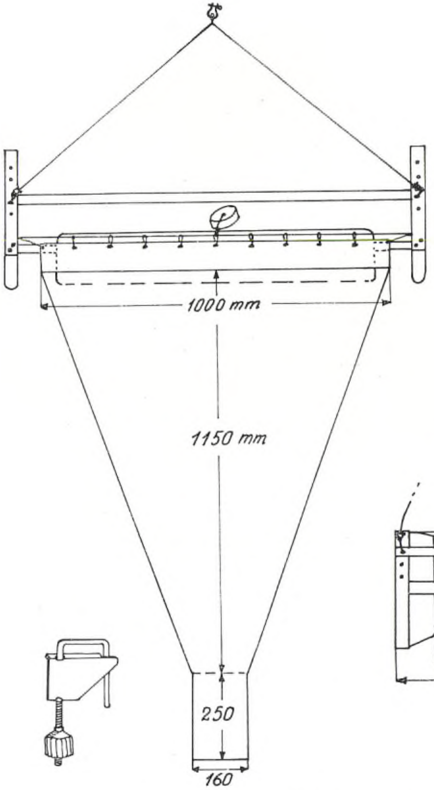


FIG. 3



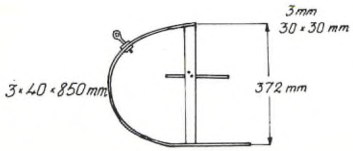
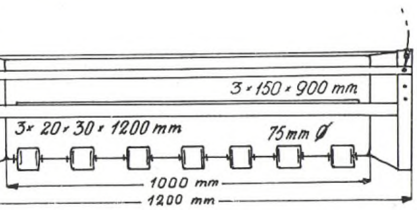
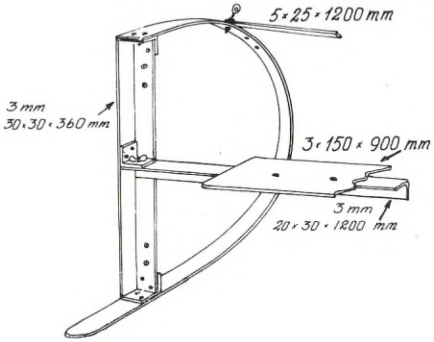


FIG. 2.





Figs. 1—3. Fig. 1. Test cage. Fig. 2. Beam trawl. Fig 3. The funnel and the chest for storing the crustaceans.

Table 2. *Mysis relicta.* Survival in cage experiments without preceding acclimatization. The electrical conductivity was measured at the surface at the time of the experiment. (cf. Fig. 4).

From lake with $\varkappa_{20}10^6$		To lake with $\varkappa_{20}10^6$		Number of tets	Number of animals	Observation time in days	Survival
Mälaren	170	Kallsjön	23	3	130	3	none
»	170	Storsjön	23	1	30	2	»
»	170	Landösjön	19	2	50	3	»
Vättern	95	Kallsjön	23	1	?	3	»
Gesunden	38	Hottöjen	30	1	30	30	good
»	38	Storsjön	23	1	40	85	»
»	38	Kallsjön	23	1	40	37	»
»	38	Torrön	17	1	10	30	»
»	38	Anjan	22	1	10	30	»
Betarsjön	28	Blåsjön	22	1	40	60	»
»	28	Storuman	38	1	40	40	»
Vättern	95	Mälaren	170	1	35	124	»
Mälaren	170	»	170	1	50	306	»
Vänern	60	»	170	1	25	16	none

to have died in the lake. Analysis of the cause of this was necessary; aquarium experiment pointed to a difference between the electrolyte content of the lakes as determining the lethality (Table 2). In these experiments water from two lakes, viz. Anjan and Vättern was mixed in different proportions. It was found that lethality increased the greater was the difference as regards the electrolyte content of the water into which the animals were put. Distilled water mixed with lake water was also used for comparison. These aquarium experiments which were of a preliminary nature were hampered by the fact that the milieu influenced the lethality.

Improved techniques may in time make possible a more complete analysis of lethality levels also after acclimatization.

3. Test cages

To avoid the difficulties connected with aquarium experiments and with a view to simulating the circumstances at the planned transplantations, the experiments were moved out into the lakes. The test cages used then were of the following simple design evolved after several years' development. A five-litre plastic pail fitted with a lid in which some ten holes have been bored makes the frame of the cage. In a number of apertures in the sides of the pail is a soldered terylene net with 1 mm meshes (see Fig. 1). Placed at a depth where the temperature is not too high, *Mysis relicta* can survive in the cage for the whole of its normal life cycle. Copulating and breeding occurs, though not at the normal frequency. These cages made it possible to do practical tests (see Table 2) at which aquarium results were confirmed. In the impounded lakes the tests were broken off after one to three months depending on ice, storm etc.

4. Technique of capture

The requirements of an instrument for capturing *Mysis relicta* (and *Pallasea quadrispinosa* and *Gammaracanthus lacustris*) are as follows. Such an instrument must:

a. catch a great many animals,
b. not damage the animals,
c. be easy to handle, usable in small boats, and collapsible,
d. not dig down into the bottom sediment.

Fig. 2 shows the type of beam trawl designed in accordance with these requirements. Because *Mysis relicta* is not caught at higher levels above bottom than 20 cm in daytime the height of the trawl can be limited. The materials are aluminium and steel or iron in the beam. For surveys one metres breadth and one millimetre meshes are used. On the beam a square of aluminium cutting downwards into the water can be fastened. In mass captures a two-metres trawl without this square is used. Two- or three-millimetre meshes are used depending on the size of the animals and the occurrence and kind of sediment. The net is made of »terylene-gardisette» which offers very little resistance to water. The cod end is made of material with a mesh so fine that the water goes through it slowly, and the animals assemble there without being pressed too hard against the material. The trawl is dragged slowly by outboard motor or by rowing (towline not thicker than 4 mm). Too high a speed seems to injure the animals, but this is mostly not visible until twenty-four hours afterwards, when abdomen usually appears white as a result of the injury. The handling must be gentle and all the time in water, but even so some mortality always appears. The time for one haul varied between 5 and 15 minutes. Up to 30 000 *Mysis relicta* were caught in one 5-minute haul using the one-metres trawl.

5. Storage and transportation of the animals

Before transport the animals have to be collected and stored in a chest. It is important to be able to fill and empty the chest in a simple manner without injuring the animals. The collapsible chest is made of "Dexion" aluminium profiles and strong one-millimetre fibre-net mesh, dimensions: $77 \times 77 \times 200$ or 300 cm. One end of the chest is covered by a large aluminium funnel (Fig. 3). The chest is floated pelagically or preferably, at a jetty. The animals are collected by means of a floating pail with a hole in its bottom and a plastic pipe down into the chest. On emptying, the light chest was raised vertically so that the animals went down with the water into a sack (1 mm mesh) tied around the funnel. Without being lifted above the water surface the sack was then put into a transport container. Experiments showed that maximum density and security in transport were attained by supplying oxygen distributed in very small bubbles.

Table 3. Data on Lakes Jansjön, Gesunden and Blåsjön. A comparison is made with Lake Mälaren at Drottningholm. (See also Table 4 and Fig. 5)

Lake	area km^2	metres above sea-level	highest shore-line	max. depth	catching depth	at relevant time and place	
						$\varkappa_{20}10^6$	pH
Jansjön	4.5	212.1	225	35	25—30	31	7.75
Gesunden	29.5	208	230	41	20—30	34—35	—
Blåsjön	39.96	435	—	147	—	22	7.60
Mälaren	1162.0	0.45	—	64	20—40	—	—

6. Transplantations from Lakes Jansjön and Gesunden to Lake Blåsjön in 1964

Jansjön and Gesunden (see Table 3) are high-altitude relict lakes situated in the River Fjällsjöälven (a tributary of the Ångermanälven) and the River Indalsälven. The chief reasons why these lakes were chosen for the collecting was that they had a low electrolyte content and that no fish parasites were found in the crustaceans caught. Lake Blåsjön, where the introduction was made, belongs to the River Faxälven (tributary of the Ångermanälven). This lake is impounded with an annual amplitude of thirteen metres, and has been closely studied by GRIMÅS (1961) and NILSSON (1961) especially as regards the damage caused to bottom fauna and fish food. The only fish species there are char and brown trout; consequently it was extremely important to check that no other species of fish were brought with the transports to Blåsjön, e.g. *Acerina cernua, Lota lota* or coregonids. The two species first mentioned were caught in the trawl, as was also *Osmerus eperlanus,* but they were easy to detect. Coregonids were never caught.

The transplantations were made during October and November 1964 partly because *Mysis relicta* was estimated to copulate at that time which would be valuable for a favorable result of the introduction and partly because of the low air temperature. At this time of the year detection of fish-fry is also easy. A disadvantage was that the capturing had to be broken off in Lake Jansjön on the 10th of November when the lake suddenly froze over. The catching work was immediately transferred southwards to Gesunden, which in its turn froze on the 19th of November. The copulating period was found to have only just started in Jansjön and Gesunden at that moment. The copulating frequency was found to be much higher in Mälaren than in these lakes at the moment of ice-formation (see Table 4, Fig. 5, cf. Table 3).

From both lakes there were transported about 1.65 million living *Mysis relicta,* 50—100,000 *Pallasea quadrispinosa* and not more than 2000 *Pontoporeia affinis.* Counting the animals is very difficult and no really accurate method of doing this is yet known. A transport density during eight hours

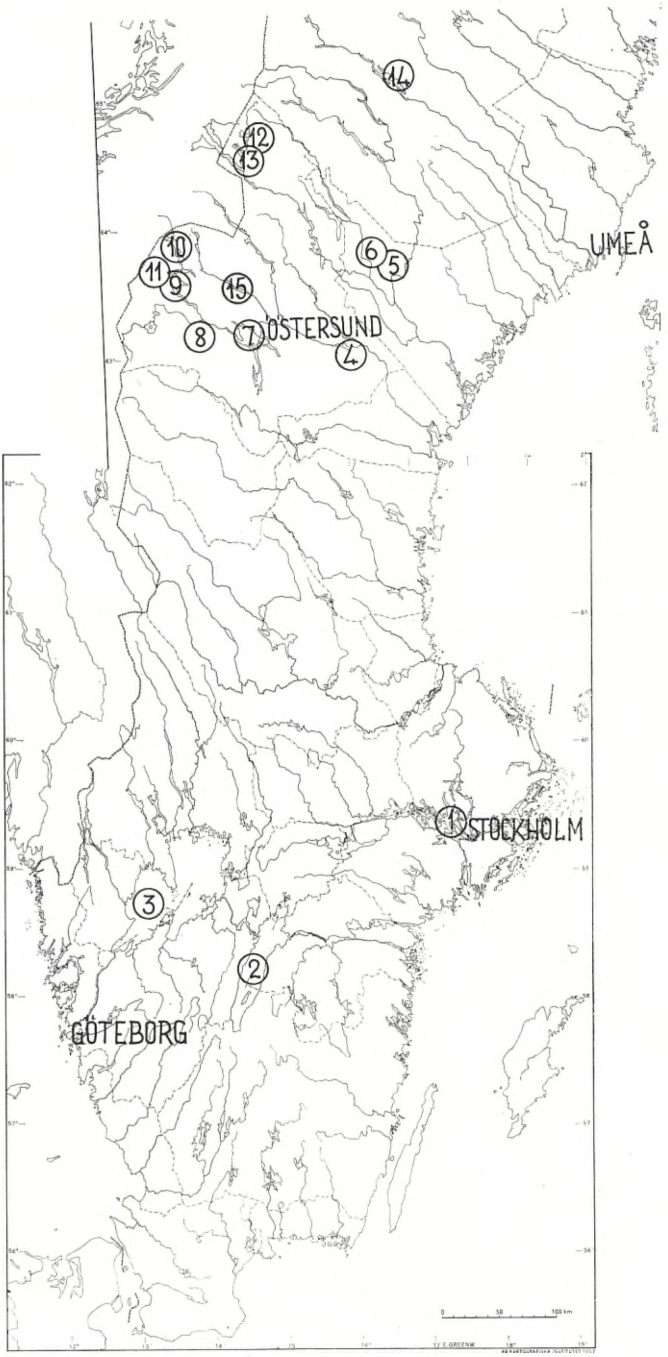


Fig. 4. Map showing lakes referred to in Tables 1, 2 and 3. 1. Mälaren, 2. Vättern, 3. Vänern, 4. Gesunden, 5. Betarsjön, 6. Jansjön, 7. Storsjön, 8. Hottöjen, 9. Kallsjön, 10. Torrön, 11. Anjan, 12. Blåsjön, 13. Kvarnbergsvattnet, 14. Storuman, 15. Landösjön.

Table 4. Number of pregnant females in relation to the time of the year, temperature and ice formation. Jansjön and Gesunden are compared with Mälaren (see diagram) where the decreasing percentage of males is also given.

Lake	Date	Temperature °C		Depth of capture	Number of *Mysis relicta* counted	Pregnant females in per cent of total number of *Mysis*		Number of *Mysis relicta* alive, when released
		surface	bottom			½ year old	1 ½ year old	
Jansjön	21.10	5,7	5,7	30	155	0	1,1	
»	28.10	5,1	5,1	30	648	0	1,8	0,80 million
»	10.11	ice	—	transport container	637	1,2	19,2	0,50 »
Gesunden	14.11	1,9	3,5	34	233	0	2,4	
»	19.11	ice	3,2	transport container	133	0	1,6	0,35 » +50—100.000 *Pallasea quadrispinosa* and 2000 *Pontoporeia affinis*

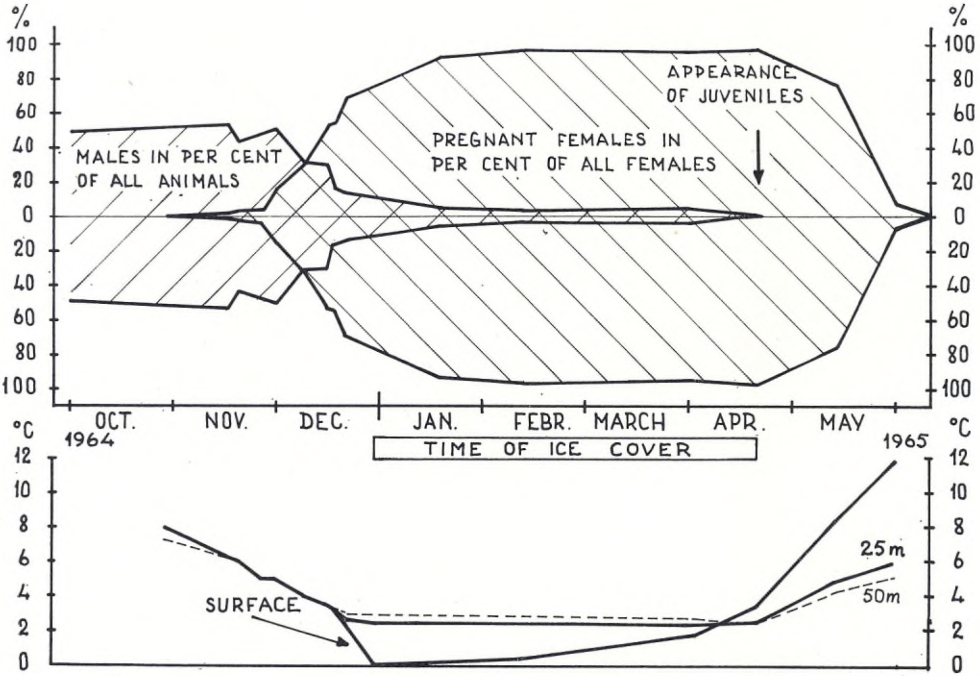


Fig. 5. Diagram showing percentage pregnant females less than one year old and water temperature in Mälaren during the winter 1964—1965. Introduction of *Mysis relicta* would theoretically give most favourable results if made when females are pregnant.

of 1.000 *Mysis* per litre of water at 6°C, and oxygen supply, was possible. At a water temperature of 1—0° and an air temperature of —18° and consequent formation of ice 700 *Mysis* and 100—200 *Pallasea* per litre were once transported during seven hours without an oxygen supply. During this transport the lorry with the containers was kept moving all the time in order to ensure oxygenation and to prevent the freezing of all the water. No mortality in connection with the transportation appeared — this was verified in cages. Forty chars were fished with gill nets during two weeks near the place of introduction in Lake Blåsjön, but none of them contained any of the introduced food organisms.

7. Summary

1. The species *Mysis relicta* Lovén is euryhaline but the different populations in Swedish lakes seem to be stenohaline. (cf. Table 2). This circumstance complicates transplantation of *Mysis relicta* between lakes with different electrolyte contents.
2. A method was worked out making it possible to carry out transplantations of *Mysis relicta, Pallasea quadrispinosa* SARS and *Gammaracanthus lacustris* SARS in a simple way. It comprises test cages, a light beam trawl and a chest for storing the animals. (The chest is easily filled and emptied.) Transport can be effected at a great density with the use of oxygen supply.
3. A transplantation to Lake Blåsjön in 1964 of about 1,65 million *Mysis relicta* and 50—100,000 *Pallasea quadrispinosa,* using this method, is described.
4. All transplantations of fish-food organisms in Sweden made by the Institute of Freshwater Research before 1965 are published (cf. Table 1).

8. References

AASS, P. 1958. The effect of impoundment on inland fisheries. *Proc. Internat. Union for Conservation of Nature and Natural Resources. RT. 7,* Id 12, 9 pp.

CLEMENS, W. A., D. S. RAWSON and J. L. MCHUGH, 1939. A biological survey of Okanagan Lake, British Columbia. *Bull. Fish. Res. Bd. Canada* No. 56, 70 pp.

DAHL, K. 1915. En studie over grundåtens eller matfloens (*Gammarus pulex*) biologi og utbredelse i Norge. Norsk Jeger- og Fisk. foren.s Tidsskr. Vol. 44, No. 5, 32 pp.

EKMAN, S. 1920. Fortpflanzung und Lebenslauf der maringlacialen Relikte und ihrer Stammformen. *Int. Rev. Hydrobiol.* Vol. 8, No. 6: 543—589.

FÜRST, M. 1964. Försök med överföring av nya näringdjur till reglerade sjöar. *Inf. från Sötvattenslaboratoriet* Nr 7. In Swedish, mimeographed.

GERD, S. W. 1954. The basic problem of introduction of Crustaceans as fish food in the lakes of the Karelo-Finnish SSR., *Petrosawodsk.* (In Russian).

GORDJEJEW, O. N. 1954. The introduction of Crustaceans as fish food in lakes of Karelo-Finnish SSR. *Papers from the conference on the problems of increasing the fish production in the waters of Karelo-Finnish SSR, Petrosawodsk.* (In Russian).

GRESE, W. N. 1955. Lakes Bolschoj and Ingol as acclimatization milieu for Coregonid fishes. *Publications of University of Tomsk.* Vol. 131. (In Russian).

— 1956. The relict Mysid (*Mysis oculata relicta* Lov.) and Pontoporeia (*Pontoporeia affinis Lindstr.*) as acclimatizationobjects *The State Research Institute of Lake and River Fisheries (GOSNIORK).* Leningrad. (In Russian).

GRIMÅS, U. 1961. The bottom fauna of natural and impounded lakes in Northern Sweden (Ankarvattnet and Blåsjön). *Rept. Inst. Freshw. Res. Drottningholm* 42: 183—237.

— 1965. Effects of impoundment on the bottomfauna of high mountain lakes. *Acta Universitatis Upsaliensis* 51, 24 pp.

HOLMQUIST, CH. 1959. Problems on Marine-Glacial Relicts on account of investigations on the genus Mysis, Lund, 270 pp.

HUITFELDT-KAAS, H. Om indsættelse av nye sorter fiskeaat i vore fiskevand. *Fiskeriinspektörens inberetning om ferskvandsfiskerierna for 1912—1913.* 11 pp. (In Norwegian).

JOFFE, I. I. 1958. Bereicherung der Bodenfauna des Cimljanschen Stausees. *Mitt. des alun. Inst. für Binnensee- und Flussfischwirtschaft.* B. XIV, 45. (In Russian).

KARPEVIČ, A. F. 1948. Results and perspectives of the acclimatization of fishes and evertebrates in USSR. *Zool. J.* Vol. XXVI, No. 6. (In Russian).

— 1960. Protection of waters against the spreading of inferior and non-useful species of fishes and evertebrates. *Ochrana prirody i ozelenie.* No. 6. (In Russian.)

— and E. N. BOKOVA. 1961. Introduction of fishes and evertebrates effected in USSR in the years 1957—59. *Ichtyology* B. I, No. 3 (20). (In Russian.)

— 1962. The acclimatization of fishes and evertebrates. *Zool. J.* B. XII, No. 7. (In Russian.)

KRUGLOVA, V. M. 1957. Bildung der Futterbasis für die Fische im Veselovschen Stausee. Arb. des Biol. Inst. der Rostover Univers. *Verlag des Ministeriums für Hochschulen der USSR.* (In Russian.)

LARKIN, P. A. 1951. Summary of investigation conducted by the Fisheries Research Group, attached to the British Columbia Game Dep. in 1949. *Ann. Rep. of the British Col. Game Com. for 1949*: 55—61.

LINDSTRÖM, T. 1962. Life history of whitefish young (Coregonus) in two lake reservoirs. *Rep. Inst. Freshw. Res. Drottningholm* No 44: 113—144.

LINN, J. D. and FRANTZ, T. C. 1965. Introduction of the Opossum shrimp (*Mysis relicta* Lovén) into California and Nevada. *Calif. Fish and Game,* 51 (1): 48—51.

MARKOWSKIJ, JU. M. 1954. The results of the work of the Hydrobiological Institute of the Academy of Science of the UKr. SSR concerning the introduction of some food-evertebrates. *The proceedings of the Conference on the problems of the acclimatization of fishes and food-evertebrates,* M. (In Russian).

MATHISEN, O. A. 1953. Some Investigations of the Relict Crustaceans in Norway with Special Reference to *Pontoporeia affinis* Lindström and *Pallasea quadrispinosa* G. O. Sars. *Nytt Magasin for Zoologi,* Vol. 1: 49—86.

NILSSON, N.-A. 1961. The effects of water-level fluctuations on the feeding habits of trout and char in the Lakes Blåsjön and Jormsjön, North Sweden. *Rept. Inst. Freshw. Res. Drottningholm* 42:238—261.

— 1964. Effects of impoundments on the feeding habits of brown trout and char in Lake Ransaren (Swedish Lappland). *Verh. Internat. Verein. Limnol.* XV: 444—453.

PIROSCHNIKOW, P. L. 1955. On the question of increasing the fauna of food organisms in lakes and reservoirs. *Zool. J.* Vol. XXXIV, No. 2. (In Russian).

RICKER, K. E. 1959. The origin of two glacial relict crustaceans in North America as related to pleistocene glaciation. *Can. J. Zool.* Vol. 37: 871—893.

RODHE, W. 1964. Effect of impoundment on water chemistry and plankton in Lake Ransaren (Swedish Lappland). *Verh. Internat. Verein. Limnol.* XV: 437—443.

RUNNSTRÖM, S. 1964. Effects of impoundments on the growth of Salmo trutta and Salvelinus alpinus in Lake Ransaren (Swedish Lappland). *Verh. Internat. Verein. Limnol.* XV: 453—461.

SEGERSTRÅLE, S. G. 1957. On the Immigration of the Glacial Relicts of Northern Europe, With Remarks on their Prehistory. *Soc. Scient. Fenn. Comment. Biol.* 16 (16), 117 pp.

— 1962. The immigration and prehistory of the glacial relicts of Eurasia and North America. A survey and discussion of modern views. *Int. Rev. Hydrob.* Vol. 47 No. 1: 1—25.

SPARROW, R. A. H., P. A. LARKIN and R. A. RUTHERGLEN. 1964. Successful Introduction of *Mysis relicta* Lovén into Kootenay Lake, British Columbia. *J. Fish. Res. Bd. Canada* 21 (5): 1325—1327.

SÖMME, S. 1935. Some small Collections of *Amphipoda* and *Mysis relicta* from *Norwegian* Lakes. *Avh. Norske Vidensk. Akad. I.* Mat.-naturvid. Klasse 1936 No. 9, 11 pp.

SÖMME, J. D. 1941. Overföringer av relikte krepsdyr — *Norsk Varekrigsforsikringsfond.* Beretning for 1940—41: 32—33. (In Norwegian).

TESCH, F. W. und G. FRIES. 1963. Die Auswirkungen des eingebürgerten Flohkrebses auf Fischbestand und Fischerei in der Weser. *Der Fischwirt* Nr 11: 319—326.

ÚŽVA, I. G. 1936. Verplanzung der Seitenschwimmer aus dem Černaja-Fluss in den Ricusee, *Fischwirtschaft* 8. (In Russian.)

ŽURAVEL, P. A. 1958. Increasing the fauna of the freshwaters of the Crimea, *Nature 6* (Of the USSR). (In Russian.)

The American crayfish *Pacifastacus leniusculus* (DANA) introduced into Sweden

By GUNNAR SVÄRDSON

PENN (1954) summarized the information regarding the spread of two American crayfish species, *Orconectes limosus* (RAFINESQUE) in Europe and *Procambarus clarkii* (GIRARD) in Japan and Hawaii.

The reason for the introduction of *Orconectes limosus* into Germany in 1890 and France in 1894 was the economic consequences of the spread of the parasitic mould *Aphanomyces astaci.* This disease appeared in Italy in 1860, in France in 1876, in Germany in 1878, in Russia in the 1880s, in Finland in 1893 and in Sweden in 1907. It is a most unusual parasite, since the mould kills not only its individual host but mostly, in a short time, the whole population of crayfish. Only rarely, and in small waters, have crayfish populations proved capable of recovery. In Sweden large bodies of water have had the disease chronically since 1907. The propagation of the disease in these cases is probably maintained by an intermittent downstream spread of crayfish from lakes situated above dams and streams, far away from the infested lakes. No alternative host has so far been found.

The exotic *Orconectes* in Europe proved to be resistant to the mould *Aphanomyces.* The size of this American crayfish, however, was rather small. This was especially important as regards the claws and the tail, the parts which are most esteemed. The flavour was also inferior to that of the *Astacus astacus. Orconectes limosus* proved to be a river-dwelling species, and to be able to stand modestly polluted water; it spread in an uncontrollable way and exterminated *Astacus* within a few years when the species met.

In Sweden crayfish are ceremonially eaten in August. They are considered a great delicacy and command high prices. The demand can not be satisfied without a huge import of crayfish from most other countries in Europe. A dense crayfish population in a Swedish lake will give the fishery-right owners (principally the land owners) a higher revenue than all the fish species of the lake taken together. Therefore, there is a strong pressure on the fishery authorities to intensify the scientific research on the *Aphanomyces* mould and to introduce exotic resistant species like the *Orconectes limosus.*

The biologists within the Fishery Board of Sweden, however, have warned against the introduction of *Orconectes limosus.* Its inferior quality does not justify the obvious risks of wide-scale competition with *Astacus* even in areas which the disease has not yet reached and where the *Astacus*-populations are therefore intact. That competition is a risk with all crayfish species

Fig. 1. A male *Pacifastacus leniusculus* from a lake near Stockholm. This specimen was brought to Sweden from California in the spring of 1960. When caught in August 1964 its total age probably was seven summers. The match box is 5 cm (2 inches).

is illustrated by the fact that the eastern *Astacus leptodactylus* has ousted the *A. astacus* in few years in many lakes and rivers of eastern and central Europe into which the *leptodactylus* has been spread by man (intentionally or by way of canals, etc.). The general distribution of the crayfish species of Europe also indicates wide-scale competition.

Preliminaries for introduction

In 1958 steps were taken to intensify research on the *Aphanomyces* and a specialist, Dr. T. UNESTAM of the Uppsala University, was employed for this work (c.f. UNESTAM 1964).

In the same year the present writer made a trip to the U.S.A. and Canada in order to survey possible candidate species for experimental introduction. He had the privilege of discussions with several specialists, among whom may be mentioned Professor H. HOBBS, Charlottesville, Virginia and Dr. C. W. THREINEN, Madison, Wisconsin.

After careful consideration of the available information on a score of species, two were selected and recommended for further experiments in Sweden, viz. *Orconectes virilis* (HAGEN) and *Pacifastacus leniusculus* (DANA) (SVÄRDSON 1959). The arguments were: *Orconectes:* lake-dwelling species of northern distribution. Probably resistant to the disease to judge from the close relationship to *O. limosus.* Flavour at least acceptable, since many Scandinavians in the Great Lake district have tested the species. On the other hand the size is small, (THREINEN 1958) especially as regards claws and tail, and the general appearance of the species is rather strange to most Swedes. *Pacifastacus:* river- or lake-dwelling species on the Pacific slope, probably adapted to milder winters than the Scandinavian ones. Nothing known about resistance. Size medium or large, claws and tail large and compare favourable with those of *Astacus.* General appearance of the species similar to the *Astacus.* Accepted as delicious by Scandinavians in the vicinity of San Francisco.

These recommendations were submitted to the Fishery Board and to the governmental authorities. The decision was taken in 1959 that the two species in question should be experimentally introduced into Sweden. Cooperation was kindly given by the Conservation Department in Madison (Dr. THREINEN) and the Californian Department of Fish and Game. The crayfish were brought to Sweden in the spring of 1960.

Results

On June 21, 1960, 70 specimens of *Orconectes virilis* were released into a small lake near the town of Hudiksvall, at the Baltic coast of Sweden. The lake had been treated with rotenone in 1959. Its name has been kept secret, in order to minimize illegal fishing or transplantations.

In spite of intensive fishing with crayfish traps in 1961—64 not a single specimen of the crayfish has been caught. It is concluded that this introduction has failed. The reasons are not known.

On May 14, 1960, 56 specimens of *Pacifastacus leniusculus* were released into a small lake near the city of Stockholm. This lake, too, is situated close to the Baltic and its name has likewise been kept secret. Like the first mentioned lake, it had been treated with rotenone in 1959. It was inhabited by *Astacus* up to 1958 but this species disappeared completely, a fact which was not realized until after the rotenone treatment. It is not known whether the *Aphanomyces* disease (which is active in nearby lakes) was responsible or, possibly, the rotenone treatment. The former alternative seems the more probable.

In 1961 test fishing in November gave no result.

In 1962 nine of the introduced specimens were caught. They had grown to a considerable size. One young crayfish of 3 cm total length was caught by hand, in early October; others were seen, but the specific identification was uncertain.

In 1963 a further 23 introduced specimens, now of large size, were trapped and 29 crayfish which, to judge by their size, were born in the lake. It thus became evident, that the species had reproduced itself and also had the capacity to survive a rather hard winter.

In 1964, 8 specimens were caught and judged to be of the California-born group. These were very large, almost at the record size for *Astacus,* and weighed 150—220 grammes (Fig. 1.). If these crayfish were two years old when imported, their total age would be 7 summers. Such a high age is known for European *Astacus* but not for American species living east of the continental divide.

The Swedish-born progeny in 1964 was rich. In August 300 specimens were trapped, a figure equivalent to the previous annual capture of *Astacus* in the lake. The growth was good, the majority of those trapped being above the 90 mm legal size limit; some measured 200—120 mm.

Two objective tests were made in August on the comparative flavour of *Astacus* and *Pacifastacus.* They were performed by trained personel at food-research institutes in Stockholm and Gothenburg. Both tests gave the same result, that there was no difference in flavour.

Dr. UNESTAM has injected the *Aphanomyces* into *Pacifastacus,* which then died by the action of the parasitic mould. But the mould seems to be blocked in its power to resolve chitin by some natural substance from the *Pacifastacus.* Several other experiments indicate that *Pacifastacus* is naturally resistant to the disease (UNESTAM 1964, 1965).

In 1964 new experiments were started, in other lakes, in order to study the interaction. Equal numbers of *Pacifastacus* and *Astacus* were introduced into a lake, that was new to both species. The distribution of crayfish along the shore of the first lake indicate that the habitat preferences of the two species are very similar (cf. ABRAHAMSSON 1964). Competition, therefore, is expected to occur. *Pacifastacus* is probably more active in daytime, which may make it more vulnerable to predators like the perch (*Perca fluviatilis*).

References

ABRAHAMSSON, S. 1964. Pågående och planerad forskning rörande ekologien hos *Astacus astacus* (LINNÉ) och *Pacifastacus leniusculus* (DANA). *Svensk Naturvetenskap 1964: 306—316.*

PENN, G. H. 1954. Introductions of American crayfishes into foreign lands. *Ecology 35 (2).*

SVÄRDSON, G. 1959. Om nordamerikanska kräftor. Redogörelse byggd på en studieresa till USA och Canada 24 okt.—9 dec. 1958. 13 pp. Mimeographed.

THREINEN, C. W. 1958. Summary of observations on the commercial harvest of crayfish in northwestern Wisconsin, with notes on the life history of *Orconectes virilis. Wisc. Conserv. Dept. Fish. Div. Misc. Rep. 2: 1—14.*

UNESTAM, T. 1964. Kräftpestproblemet (The problem of the crayfish plague). *Svensk Naturvetenskap 1964*: 317—327.

— 1965. Studies on the crayfish plaque fungus, *Aphanomyces astaci.* I. Some factors affecting growth in vitro. Physiologia Plantarum 18 (2).

The Coregonid Problem. VII

The isolating mechanisms in sympatric species

By Gunnar Svärdson

Contents

I. Introduction

In recent years several authors in Europe and North America have described the coregonine fishes as groups of sibling species, evolved in allopatric isolation during glacial periods. After the retreat of the glaciers, the incipient species met sympatrically. They are often capable of coexisting, sharing parts of the same environment. Sometimes, however, they cannot maintain their genetical integrity but form introgressed populations (Svärdson 1957 a, Lindsey 1963, Fenderson 1964). Some authors find that the introgression is due mainly to human interference by artificial propagation (Dottrens 1959) or changed environments through pollution (Karbe 1964 b) or increased fishing pressure (Smith 1964). There are a few authors, however, who still adhere to a morphological species concept (Gasowska 1960, Reshetnikow 1963).

The tentative grouping of numerous coregonine forms, some of which were poorly described, into a few species (Svärdson 1957 a) served to prompt further information about forms well known in some parts of the

Palearctic but less known in other regions (GASOWSKA 1960, LINDSEY 1962, RESCHETNIKOW 1963). The taxonomic aspect of whitefish variability, however, seems at present less important than its contribution to evolutionary thought. MAYR (1964) has stressed that introgression is a rare phenomenon in the animal kingdom. This is probably true. But the introgression of *Coregonus* is by no means unique, there are parallels in *Salvelinus, Clupea* and other well-known fish of economic importance. The slow understanding of introgression in forms so intensively studied as these indicates that similar phenomena may be widespread in lesser studied fish.

The species concept and the isolating mechanisms of the coregonid fish are the main theme of this paper. In Sweden it has been studied for decades by means of transplantations, hybridization and population experiments. Most of the experiments have been performed at the Kälarne Field Research Station, situated in the province of Jämtland in central Sweden. The Gimå River lakes, discussed in another section, have been selected for intensive population studies because they lie close to the Kälarne station. The rich material on scales and growth data, year-class fluctuations and competition will be left for further reports, apart from some details related to the main theme of this paper.

A dept of gratitude is owed to Mr. ELOF HALVARSSON, head of the Kälarne station, for his never failing interest in the experiments, for his skill in fishing as well as rearing fry to older fish and for his remarkable ability to transport fish alive through forests where there are no roads.

II. Material and lakes

Lake Kölsjön (Table 1). On November 11, 1947, Mr. E. HALVARSSON stripped eggs and milt of the Baltic whitefish (*C. lavaretus*) running the Indalsälven river for spawning. In summer this species roams widely in the Baltic Sea (LINDROTH 1957). The eggs were taken at Boda, some 50 km from the

Table 1. Gillraker distribution of *C. lavaretus* in Lake Kölsjön. The species was transplanted into the lake from the mouth of the Indalsälven river in 1948.

	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	n	x̄
River Indalsälven[1] 1950—1953	—	—	2	8	14	35	60	78	79	60	54	36	15	10	4	—	—	—	455	31.0
Lake Kölsjön 1955	—	—	—	1	7	10	9	15	20	22	15	6	2	—	—	—	—	—	107	30.8
,, ,, 1956	—	1	—	2	4	8	8	20	14	15	13	8	5	1	—	—	—	—	99	31.0
,, ,, 1958	—	—	—	3	10	13	23	21	20	16	4	3	—	—	—	—	—	—	113	29.9
,, ,, 1961	—	—	—	—	5	8	17	19	20	14	14	4	4	—	—	—	—	—	105	30.7
.. ,, 1962	—	—	1	3	6	10	13	17	12	16	12	11	2	1	1	—	—	—	105	30.8
,, ,, 1963	—	—	—	—	8	7	12	20	20	9	11	9	2	1	1	—	—	—	100	30.7
,, ,, 1964	—	—	—	1	3	6	10	14	23	22	19	2	5	2	1	1	—	—	109	31.4
Lake Kölsjön Σ	—	1	1	10	43	62	92	126	129	114	88	43	20	5	3	1	—	—	738	30.8

[1] Includes material from LINDROTH (1957).

river mouth. The eggs eyed out at Kälarne in late January and on April 12 some 185,000 eggs were put into Lake Kölsjön. They were distributed to several gravel parts of the lake's shore, through the ice, and over a depth of 0.5—1.5 m. Some thousands were put into a small creek running down to the lake. It was estimated that hatching should occur in Lake Kölsjön about May 1, 1948.

Lake Kölsjön has an area of 3,500 hectars, an altitude of 800 metres and feeds the Kölån—Fjätälven river, a tributary of the Österdalälven. It lies 200 km SW of the mouth of the Indalsälven; it is a mountain lake and offers the whitefish a colder and less nutritious habitat than the Baltic Sea does. The maximum depth of Lake Kölsjön is 17 metres and a considerable part of it has a depth of 10 metres.

There were no whitefish species in Lake Kölsjön in 1948. The survival of the introduced population was good and a lot of fish were taken in gill nets by the local inhabitants in the period 1949—1954. Scales have been sampled from 1955 onwards. The first spawning of the introduced whitefish stock was in the autumn of 1950 but the 1951 and 1952 classes were small. The 1953 class, however, was abundant. Growth is still excellent but will probably slow down as the population becomes more crowded. Grayling (*Thymallus thymallus*) has been ousted and perch (*Perca fluviatilis*) is reduced by the whitefish.

The Indalsälven stock spawns during the first half of November (LINDROTH 1957) while the Kölsjön population spawns in the last half of October.

The samples recorded in Table 1 were fished by means of a standard set of gill nets of different mesh sizes. The same kind of standard set has been used also in some, but not all, of the lakes mentioned below.

Lake Stora Skeppsträsket (Table 2). This lake belongs to the system of the Malå river, a tributary of the Skellefte river. The small-sized whitefish of the lake (*C. oxyrhynchus*), called *löja*, has been dealt with earlier (SVÄRDSON 1951, 1957 b).

Mr. R. GYDEMO, fishery officer of the district, has fished the *löja* for many years. It spawns at Christmas time and there are often severe cold spells at this time of the year. In 1951 Mr. GYDEMO hybridized the *oxyrhynchus* in Lake Skeppträsket with a bigger species (*C. nasus*) living sympatrically in Skeppträsket but also allopatrically in the neighbouring Lake Brunträsket (cf. SVÄRDSON 1951). For practical reasons, the spawning grounds being better localized, the Brunträsket population was used as the other parent of the hybrids. The eggs, numbering 5,000, were sent to Kälarne, where they hatched. In the spring of 1952, the fry was released in a small tarn, called Grästjärn.

There are no spawning grounds for whitefish in the Grästjärn tarn. Ripe fish, however, were netted by Mr. HALVARSSON in the autumn of 1954 and

Table 2. Gillraker distribution of *C. oxyrhynchus* and *C. nasus*, Lake Stora Skeppträsket, their F1 hybrids in the tarn Grästjärn and the F2 in three tarns in the vicinity of Kälarne.

		19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	n	x̄
C. oxyrhynchus	Aug. 1913	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3	4	5	6	5	3	2	2	—	—	31	40.0
	Dec. 1946	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	2	3	2	1	—	—	1	—	—	11	38.8
	Dec. 1949	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3	8	17	25	16	10	9	4	—	—	—	93	39.4
	Dec. 1950	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	7	9	21	19	12	9	3	2	—	—	85	39.7
	Dec. 1953	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	12	15	9	21	18	12	7	2	1	—	100	39.9
	Dec. 1954	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	7	14	7	26	14	15	8	4	2	1	100	40.0
	Dec. 1964	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	5	13	18	28	19	10	6	4	1	—	105	40.1
Σ		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	5	10	42	74	88	118	79	58	30	15	4	1	525	39.9
C. nasus	Oct. 1948	1	2	3	9	5	5	9	5	4	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	45	23.9
F1 Grästjärn ..	1952 O+	—	—	—	—	—	—	—	—	—	—	—	—	5	7	12	7	2	2	—	—	—	—	—	—	—	—	—	—	35	33.0
	1953 I+	—	—	—	—	—	—	—	—	1	1	—	6	11	20	28	30	20	16	8	—	—	—	1	—	—	—	—	—	142	33.6
	1954 II+	—	—	—	—	—	—	—	—	—	—	1	2	5	14	14	15	20	7	2	—	—	—	—	—	—	—	—	—	80	33.6
	1956 IV+	—	—	—	—	—	—	—	—	—	—	—	1	—	1	1	—	1	2	—	—	—	—	—	—	—	—	—	—	6	33.7
	1958 VI+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	2	33.5
Σ F1		—	—	—	—	—	—	—	—	1	1	1	9	21	42	56	53	43	27	10	—	—	—	1	—	—	—	—	—	265	33.5
F2 Grästjärn ...	1955 O+	—	—	—	—	—	—	—	1	2	2	7	12	7	5	9	2	3	—	—	—	—	—	—	—	—	—	—	—	50	30.9
	1956 I+	—	—	—	—	—	—	—	1	3	1	6	17	17	13	7	7	3	2	—	—	—	—	—	—	—	—	—	—	77	31.3
	1958 III+	—	—	—	—	—	—	—	—	—	6	8	4	16	10	13	4	6	2	—	—	—	—	—	—	—	—	—	—	69	31.6
Rörtjärn ...	1955 O+	—	—	—	—	—	—	—	—	—	2	—	1	—	1	3	—	—	—	—	—	—	—	—	—	—	—	—	—	7	31.0
	1956 I+	—	—	—	—	—	—	—	—	—	—	2	4	1	4	2	1	2	—	—	—	—	—	—	—	—	—	—	—	16	31.7
Abborrtjärn	1956 I+	—	—	—	—	—	—	—	—	—	1	—	2	2	4	2	—	3	1	—	—	—	—	—	—	—	—	—	—	15	32.3
	1958 III+	—	—	—	—	—	—	—	—	—	1	—	1	2	1	3	2	1	—	—	—	—	—	—	—	—	—	—	—	11	32.2
Σ F2		—	—	—	—	—	—	—	2	5	13	23	41	45	38	39	16	18	5	—	—	—	—	—	—	—	—	—	—	245	31.4

Table 3. Gillraker distribution of *C. oxyrhynchus* and *C. albula*, Lake Åsnen, their F1 hybrids in the tarn Gravtjärn and the F2 and F3 generations in the tarn Ö. Vontjärn and Lakes Öratjärn and S. Stensjön.

		28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	n	x̄
C. oxyrhynchus	Nov. 1951	—	—	—	—	1	4	5	9	20	10	6	2	1	—	—	—	—	—	—	—	—	—	58	35.9
C. albula	Nov. 1951	—	—	—	—	—	—	—	—	—	—	2	1	1	5	8	10	12	6	3	2	1	—	51	43.2
F1 Gravtjärn	O+	—	—	—	—	—	1	5	11	13	33	35	20	16	11	7	3	—	2	—	—	—	—	157	38.2
	I+	—	—	—	—	—	—	—	3	—	10	4	7	2	8	9	3	2	—	2	—	—	—	50	39.9
	II+	—	—	—	—	1	—	—	2	7	10	11	16	5	3	1	2	2	2	—	—	—	—	62	38.6
Σ F1		—	—	—	—	1	1	5	16	20	53	50	43	23	22	17	8	4	4	2	—	—	—	269	38.6
F2 Ö. Vontjärn	I+	—	—	1	—	6	8	6	7	6	7	10	7	2	1	2	—	—	—	—	—	—	—	63	36.0
	II+	—	—	—	2	4	5	9	21	23	29	18	12	7	3	2	1	—	—	—	—	—	—	136	36.6
Σ Ö. Vontjärn		—	—	1	2	10	13	15	28	29	36	28	19	9	4	4	1	—	—	—	—	—	—	199	36.4
F2 Öratjärn	III+	—	—	—	2	5	10	18	22	28	21	20	12	2	1	1	—	—	—	—	—	—	—	142	36.0
	IV+	—	—	—	—	—	1	3	13	16	18	10	7	2	4	1	—	—	—	—	—	—	—	75	36.9
	V+	—	—	—	—	—	1	2	4	14	11	4	3	2	1	2	—	—	—	—	—	—	—	44	37.0
	VI+, VII+	—	—	—	—	—	—	—	2	1	—	1	—	1	—	—	—	—	—	—	—	—	—	5	36.8
Σ Öratjärn		—	—	—	2	5	12	23	41	59	50	35	22	7	6	4	—	—	—	—	—	—	—	266	36.4
F2 S. Stensjön	II+	—	1	2	2	10	10	11	12	15	15	8	4	—	1	—	—	—	—	—	—	—	—	91	35.1
	III+	—	—	—	1	2	6	6	9	22	25	21	8	8	1	1	—	—	—	—	—	—	—	110	36.7
	IV+	—	—	—	—	—	1	11	13	11	27	20	6	3	2	—	—	1	—	—	—	—	—	95	36.8
	V+, VI+	—	—	—	1	—	2	6	15	13	13	9	3	6	2	1	—	—	—	—	—	—	—	71	36.6
Σ S. Stensjön		—	1	2	4	12	19	34	49	61	80	58	21	17	6	2	—	1	—	—	—	—	—	367	36.3
Σ F2		—	1	3	8	27	44	72	118	149	166	121	62	33	16	10	1	1	—	—	—	—	—	832	36.4
F3 Öratjärn	1961	—	—	—	—	—	1	1	2	1	4	3	—	—	—	—	—	—	—	—	—	—	—	12	36.3
	1962	—	—	—	—	—	3	1	10	14	11	12	3	2	2	—	—	—	—	—	—	—	—	56	36.8
	1963	—	—	—	—	2	5	6	9	13	15	11	13	7	2	2	—	—	—	—	—	—	—	85	37.0
	1964	—	—	—	—	—	1	4	5	17	27	22	15	10	2	—	—	—	—	—	—	—	—	103	37.5
Σ Öratjärn		—	—	—	—	2	10	12	26	45	57	48	31	19	6	2	—	—	—	—	—	—	—	258	37.1
F3 S. Stensjön	1962	—	—	—	—	—	—	1	2	1	5	1	1	—	—	—	—	—	—	—	—	—	—	11	36.5
	1963	—	—	—	1	1	1	3	6	11	11	9	1	3	1	—	—	—	—	—	—	—	—	48	36.5
	1964	—	—	1	—	3	1	7	11	19	23	10	11	3	4	1	—	—	—	—	—	—	—	94	36.7
Σ S. Stensjön		—	—	1	1	4	2	11	19	31	39	20	13	6	5	1	—	—	—	—	—	—	—	153	36.6
Σ F3		—	—	1	1	6	12	23	45	76	96	68	44	25	11	3	—	—	—	—	—	—	—	411	36.9

Table 4. Gillraker distribution of *C. pidschian* and *C. peled* in Lakes Uddjaur-
were introduced as

		14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
C. pidschian	Dec. 1953	—	—	1	2	4	5	3	2	—	—	—	—	—	—	—	—
C. peled	Dec. 1953	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F1 N. Stensjön	O+	—	—	—	—	—	—	—	—	1	1	—	1	3	9	8	7
	I+	—	—	—	—	—	—	—	—	—	—	—	—	—	2	3	2
	II+	—	—	—	—	—	—	—	1	—	—	—	—	5	17	27	17
	IV+	—	—	—	—	—	—	—	—	—	—	1	1	7	13	26	21
	V+	—	—	—	—	—	—	—	—	—	—	—	—	3	9	8	18
	VI+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	15
	VII+	—	—	—	—	—	—	—	—	—	—	—	1	—	1	4	3
	VIII+	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	4
	IX+	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	2
Σ F1		—	—	—	—	—	—	—	1	1	1	1	3	18	53	86	89
F2 Stensjön	1958	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—
	1959	—	—	—	—	—	—	—	—	—	—	6	11	10	15	14	9
	1960	—	—	—	—	—	—	—	1	2	—	4	2	4	4	3	3
	1961	—	—	—	—	—	—	—	1	—	3	2	3	7	15	12	6
	1962	—	—	—	—	—	—	—	—	—	1	2	8	3	10	12	11
	1963	—	—	—	—	—	—	—	—	1	1	3	4	7	5	9	16
Σ F2		—	—	—	—	—	—	—	2	3	5	17	29	32	49	50	45

in later years, and F2-fish were produced. The fry was again released in the Grästjärn tarn, as well as in the similar tarns Rörtjärn and Abborrtjärn.

Lake Åsnen (Table 3). This lake of 15,000 hectars, altitude 138 metres, lies in southern Sweden. It feeds the famous salmon river Mörrumsån. The lake is shallow, its maximum depth being only 14.2 metres. There is one whitefish species (*C. oxyrhynchus*), locally called *ranning,* as well as a cisco population (*C. albula*) in the lake. Their spawning periods partly overlap, a circumstance which prompted artificial crossings. Spontaneous hybrids between whitefish and cisco are difficult to identify, since they are confused with other whitefish species. In a few cases in other lakes, however, when the cisco lives sympatrically with *C. pidschian,* stray hybrids have been positively identified.

Mr. B. JOHANSSON, fishery officer of the district, fertilized cisco eggs by whitefish milt in Lake Åsnen in November 1949. It was later found at Kälarne, however, that the fish were pure ciscoes. Probably the eggs were fertilized by sperm, swimming on the wet gill nets when the catch was brought to shore. This false »parthenogenesis» demonstrated what probably happened to the fish discussed by MELANDER and MONTÉN (1950). Using particular care the experiment was repeated in November 1952. This time, real hybrids were formed. The fry was put into a small tarn in the Kälarne area, called Gravtjärn, where the fish could not spawn. Ripe fish were netted in the autumns of 1956 and 1957 and an F2 generation was produced. These F2 fry were first put into a further tarn, Ö. Vontjärn, but were later reared to fingerlings at Kälarne.

Storavan, their F1 hybrids and F2 generation in Lake N. Stensjön. The F1 fingerlings in 1954.

30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	n	x̄
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	17	18.8
—	—	—	—	—	—	—	—	—	—	1	—	—	3	6	2	1	7	4	1	1	26	45.7
11	8	4	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	56	29.0
5	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	29.4
19	12	9	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	112	29.1
16	12	5	2	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	107	29.0
14	13	10	6	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	82	29.8
11	8	4	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	49	29.9
1	1	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	14	29.2
1	3	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12	30.1
2	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	29.8
80	62	34	17	9	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	456	29.3
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	25.5
10	6	9	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	94	28.0
9	4	6	5	3	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	52	29.1
12	10	1	5	4	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	83	28.7
8	12	6	8	3	3	2	1	1	1	—	—	—	—	—	—	—	—	—	—	—	92	29.7
17	23	12	5	2	3	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	109	29.7
56	55	34	25	12	9	3	2	1	1	—	—	—	—	—	—	—	—	—	—	—	430	29.1

In October 1957, 5,500 one-summer-old F2 hybrids were transported to Lake Öratjärn. This lake has an area of 35 hectars, a maximum depth of 16 metres, and offers the hybrid whitefish×cisco a good feeding habitat and spawning grounds. Lake Öratjärn, which is situated in the royal forestry park of Gullmyrberget, is situated 5 km from the centre of Loos. In Lake Öratjärn the hybrid fish have to compete with pike, perch and some trout.

On September 27, 1958, 5,400 one-summer-old F2 hybrids were transported from Kälarne to Lake S. Stensjön, not far from Lake Öratjärn, in the forestry park of Turinge. Lake S. Stensjön has an area of 40 hectars and a maximum depth of 12 metres. The competing species are again pike, perch and trout. There are good spawning grounds for the whitefish×cisco hybrids in this lake.

All the samples from Lake Åsnen, and the tarns Gravtjärn and Ö. Vontjärn as well as Lakes Öratjärn and S. Stensjön are included in Table 3.

Lakes Uddjaur-Storavan (Table 4). In the upper part of the River Skellefteälv, there are three large lakes, Hornavan—Uddjaur—Storavan forming a water area of 66,100 hectars. They are connected by short, open streams. The whitefish species of the lakes have been described earlier (SVÄRDSON 1953). The food competition between the species has been dealt with by LINDSTRÖM and NILSSON (1962).

Mr. A. NORDIN, then a member of the staff of the Freshwater Institute, trapped some ripe males of *C. peled* in the stream between Uddjaur and Storavan in November 1953 and kept them alive until *C. pidschian* spawned in Lake Storavan in late December. The fertilized hybrid eggs were sent to

Table 5. Gillraker distribution in samples of spawning *C. pidschian, C. nasus,* and *C. lavaretus* in Lake Idsjön, Gimå river system.

		15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
C. pidschian	Dec. 1952	—	—	—	—	—	4	3	3	—	—	1	1	—	—	—	—	—	(1)	—	—	—	—	—	—	—	—	—	—	—
	Dec. 1956	—	1	4	13	15	31	27	10	5	2	—	2	—	—	1	—	(1)	—	[1]	—	(1)	(1)	—	(1)	—	—	—	—	—
	Jan. 1957	—	1	3	3	4	5	6	2	1	2	—	1	1	—	—	—	—	—	[1]	—	[1]	—	—	—	—	—	—	—	—
	Dec. 1958	1	2	12	8	20	27	18	11	6	1	2	1	—	—	—	—	—	—	[1]	—	—	—	—	[1]	—	—	—	—	—
	Dec. 1960	—	1	5	12	22	21	9	7	2	2	2	—	—	—	—	—	—	—	—	—	—	—	[1]	—	—	—	—	—	—
	Dec. 1961	—	—	1	4	7	15	11	11	6	3	1	—	—	—	—	—	—	—	[1]	—	—	—	—	—	—	—	—	—	—
	Dec. 1962	—	—	—	2	8	14	9	9	3	2	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Dec. 1963	—	—	3	10	11	13	14	8	3	4	—	—	1	1	—	—	[1]	1	—	—	—	—	—	—	—	—	—	—	—
	Dec. 1964	—	—	1	3	3	7	3	3	1	2	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C. nasus	Nov. 1950	—	—	—	—	—	—	1	3	4	6	12	11	8	4	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Oct. 1952	—	—	—	—	—	—	—	2	4	15	19	16	16	10	5	6	1	[1]	[2]	(3)	—	(1)	(1)	—	(1)	—	—	—	—
	Oct. 1953	—	—	—	—	1	—	4	5	27	46	75	55	51	25	9	11	5	—	[1]	—	—	—	—	—	—	—	—	—	—
	Oct. 1954	—	—	—	—	—	—	5	13	28	34	66	55	49	31	13	7	2	2	—	(1)	(1)	—	(1)	—	—	—	—	—	—
	Oct. 1955	—	—	—	—	1	1	2	10	21	50	55	61	42	31	15	5	4	2	—	[2]	(1)	(2)	(1)	—	—	—	—	—	—
	Oct. 1956	—	—	—	—	—	—	5	11	28	42	62	79	51	35	22	10	8	3	1	—	—	—	—	—	(1)	—	—	—	—
C. lavaretus	Nov. 1947	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	3	2	4	3	5	2	—	—	1	—
	Oct. 1948	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	3	9	11	13	24	12	8	8	3	3	—	—
	Nov. 1950	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	5	3	8	11	10	7	3	3	1	—	1	—
	Oct. 1954	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	11	18	34	38	51	51	35	28	15	13	2	1
	Oct. 1955	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3	11	27	36	44	46	59	37	23	9	2	2	—

( ) = egg-predators
[ ] = "intra-lake-transplanted" fish

Table 6. Gillraker distribution in samples of spawning *C. oxyrhynchus* and *C. lavaretus* in Lake Ansjön, Gimå river system. Fishing before spawning periods in 1964 caught predominantly *C. oxyrhynchus*.

		21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	n	x̄
C. oxyrhynchus .	Febr. 1951	—	—	—	—	—	—	—	—	—	—	1	1	3	12	15	21	20	16	17	13	6	2	—	—	—	127	37.1
	Jan. 1953	—	—	—	—	—	—	—	—	—	—	2	9	14	13	16	14	17	9	5	2	2	—	—	—	—	103	35.4
	Febr. 1953	—	—	—	—	—	—	—	—	—	1	—	3	6	7	8	15	14	13	8	—	1	—	—	1	—	77	36.2
	Jan. 1954	—	—	—	—	—	—	—	—	—	1	—	3	7	6	19	20	24	19	14	5	2	1	1	—	—	122	36.6
	Febr. 1955	—	—	—	—	—	—	—	2	—	3	3	7	10	12	17	18	17	7	7	2	—	1	—	—	—	106	35.2
	Febr. 1956	—	—	—	—	—	—	—	—	1	2	8	3	11	16	24	18	9	16	5	2	—	—	—	—	—	115	35.2
Σ		—	—	—	—	—	—	—	2	1	7	14	26	51	66	99	106	101	80	56	24	11	4	1	1	—	650	36.0
C. lavaretus	Jan. 1953	1	—	—	—	1	—	—	—	1	2	3	12	17	21	25	16	10	3	2	—	—	—	—	—	—	114	34.2
	Febr. 1953	—	—	—	—	—	—	—	—	—	—	3	1	3	7	3	2	2	1	1	1	—	—	—	—	—	24	34.6
	Jan. 1954	—	—	—	—	—	—	—	—	2	5	6	9	14	22	20	5	5	3	2	1	—	—	—	—	—	94	33.9
	Jan. 1955	—	—	—	—	—	—	—	—	3	2	4	7	3	3	7	5	3	1	—	1	—	—	—	—	—	39	33.6
	Febr. 1955	—	—	—	—	—	—	—	1	—	—	2	2	4	5	4	3	3	—	—	—	—	—	—	—	—	24	34.0
	Febr. 1956	—	—	—	—	—	—	1	—	2	5	8	8	21	10	6	12	2	1	2	—	—	—	—	—	—	78	33.4
	Febr. 1958	—	—	—	—	—	—	—	—	1	2	7	12	11	8	3	3	6	2	—	—	—	—	—	—	—	55	33.4
Σ		1	—	—	—	1	—	1	1	9	16	33	51	73	76	68	46	31	11	7	3	—	—	—	—	—	428	33.8
	Oct. 1964	—	—	—	—	—	—	—	—	1	—	4	10	24	29	32	49	57	42	29	11	6	4	2	—	—	300	36.4

Table 7. Gillraker distribution in samples of (mostly) spawning *C. pidschian*,
lings of *pidschian* and hybrids *pidschian* × *oxyrhyn-*

		15	16	17	18	19	20	21	22	23	24	25	26
C. pidschian	Febr. 1959	—	2	2	6	13	6	3	1	—	—	—	—
	Jan. 1964	—	—	1	1	4	7	5	—	—	—	—	—
	Febr. 1965	—	—	3	8	7	6	3	4	—	—	—	—
fingerlings, 66 cm pond, Kälarne	Oct. 1964	—	—	12	25	28	28	4	2	—	—	—	—
C. nasus	Jan. 1956	—	—	1	4	12	14	21	26	21	15	4	—
	Oct. 1956	—	—	—	—	2	4	4	—	4	1	3	2
C. oxyrhynchus	Febr. 1957	—	—	—	—	—	1	1	—	—	—	—	—
	Jan. 1964	—	—	—	—	—	—	—	—	—	—	—	—
	Febr. 1965	—	—	—	—	—	—	—	—	—	—	—	—
C. pidschian, fingerlings 102—103 mm, pond, Kälarne	Oct. 1964	—	6	23	99	196	197	136	44	12	1	—	—
	Oct. 1964	1	1	21	87	175	218	143	41	8	—	—	—
F1-hybrids *pidschian* × *oxyrhynchus* fingerlings 107—108 mm, pond, Kälarne	Oct. 1964	—	—	—	—	—	—	—	—	—	—	—	4
	Oct. 1964	—	—	—	—	—	—	—	—	—	—	—	1

Kälarne and 5,000 fry hatched in May 1954. They were raised to fingerlings in a pond and 3,500 were transported by car on September 30 (in an exceptionally early snowstorm involving blocked roads) to Lake N. Stensjön.

Lake N. Stensjön has an area of 125 hectars, and belongs to the Stensjön forestry park, Hogdal, in the parish of Los. The lake bottom is mostly gravel; the maximum depth is 18 metres. It offers the whitefish a good habitat and spawning grounds. Stunted perch dominated the lake in 1954 — they have since been reduced — and there were also some pike, a very few trout and many burbot.

The F1 hybrids had a very rapid growth in the lake. They spawned for the first time in 1957. Thus the first year-class of F2 fish hatched in the spring of 1958.

The Gimå River lakes (Tables 5, 6 and 7). The whitefish species of Lake Idsjön, close to the Kälarne station, have been dealt with earlier (SVÄRDSON 1953). A very rich material of scales and gillraker counts has been taken from this lake. There are three species in Lake Idsjön (Table 5).

Lake Ansjön has also been sampled intensively, since it was found that there were two introgressed species in the lake. One is larger than the other, has fewer gillrakers and spawns closer to the shore as well as earlier in the season. The difference between the species, however, is slight and there are many intermediate fish and local populations (Table 6).

Lake Locknesjön is the largest of the lakes concerned and has three species of whitefish (SVÄRDSON 1959). At first only two were found (SVÄRDSON 1957 a) and then the gillrakers indicated an exceptional, small-sized

C. nasus and *C. oxyrhynchus* in Lake Locknesjön, Gimå river system. Finger-
chus, raised in ponds at Kälarne, are also included.

27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—
—	—	—	—	—	—	—	—	—	—	1	1	1	3	3	6	1	4	1	1	—	—	—
—	—	—	—	1	—	—	—	—	—	3	2	15	19	12	12	17	10	6	—	—	1	—
—	—	—	—	—	—	—	—	—	—	2	4	7	12	15	15	17	13	7	7	1	—	—
—	—	—	—	—	—	—	—	—	—	2	1	2	1	8	6	6	5	5	—	2	1	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
25	82	201	202	159	80	25	5	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
18	80	198	215	154	98	34	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

pidschian in the lake. Later, however, the real *pidschian* was localized. Since gillraker distribution and spawning periods were suitable for experiments *pidschian* eggs were fertilized by *oxyrhynchus* sperm in February 1963. The parent species have such different gillraker counts (19 and 42 respectively) that every F1 specimen could be identified even when raised together with true *pidschian* (Table 7). Heterosis could be studied when 3,500 *pidschian* fry were released with 3,500 hybrid fry in one pond at Kälarne in the spring of 1964. In autumn, a sample of 3,000 fingerlings was secured, preserved and later studied in the laboratory. The gillrakers of the fingerlings were counted by two technical assistants, working independently, in order to check the influence of the human factor also.

III. Results

Hybrid viability. It has long been known that artificially produced hybrids between coregonine species have a good viability. GASOWSKA (1958) cites several Russian authors on the subject, viz. CALIKOV, TICHIJ, DRJAGIN, BEREZOVSKIJ and NESTERENKO. GASOWSKA herself studied the hybrid between whitefish and cisco. In North America the same results were reported by MOENKHAUS (1910) and GARSIDE and CHRISTIE (1962).

In six experiments, hybrids have been produced between pairs of sympatric *Coregonus* species in Sweden. Two experiments were fully reported earlier (SVÄRDSON 1957 a), while the other four have been followed up later (Tables 2, 3, 4, and 7). These Swedish experiments prove, as do those performed abroad, that hybrid embryonic mortality is as low as that of intraspecific fertilization.

In the literature cited above there are some statements that the hybrids have superior growth and survival. This heterosis, however, cannot be proved with certainty until adjustment has been made for all the environmental conditions.

The whitefish species of Lake Locknesjön were suitable for such an experiment (Table 7). Thanks to the very different gillraker numbers of *pidschian* and *oxyrhynchus* and their overlapping spawning periods, eggs of *pidschian* females could be fertilized by *pidschian* as well as *oxyrhynchus* sperm. Since *pidschian* normally has considerably larger eggs, the reciprocal crossing would most probably give a less favourable relation between the myomeres of the fry and the amount of yolk in the hybrid fish. This might interfere with survival or growth (GARSIDE and FRY 1959).

The same number of *pidschian* and hybrid fry were allowed to live and compete in a natural pond for one summer. Later two technical assistants at the Institute each independently studied a sample of 1,500 fingerlings:

	First assistant			Second assistant		
	Number of fish	Rakers	Fish-length mm	Number of fish	Rakers	Fish-length mm
Pidschian	714	19.6	102.3	695	19.7	103.1
F1 hybrids	786	29.9	107.2	805	30.0	108.0

There were slight individual differences between the two assistants in counting gillrakers and, especially, recording the total length of the fish. The heterosis effect, however, was significant in the two samples. The assistants found that the F1 hybrids had a 10—16 per cent better survival and the total length of the hybrids was, in both assistants' measurements, 4.8 per cent greater.

Since most of the pre-adult mortality is passed when whitefish are one summer old, the result indicates that in nature the interspecific hybrids probably have a 10—20 per cent better survival than the parent species and a more rapid growth rate. This better growth may give the hybrids an earlier sexual maturity than that of the parent fish. In whitefish males the maturity comes after 2—4 summers growth, in the females one year later.

Hybrid fertility. Some of the authors describing the viability of the coregonine hybrids have also commented upon their fertility, which was said to be good. In a general way this is no doubt true. Tables 2—4 demonstrate that an F2 generation could be raised in all three cases studied.

In Lake N. Stensjön (table 4) the introduced F1 hybrids reproduced by natural spawning, and by means of scale-reading in the laboratory the F1 fish could be separated from F2 fish. The gillrakers of 456 F1 fish could be recorded and compared to the rakers of their progeny, comprising

Table 8. Growth (total length in mm) as calculated from scales of F1 hybrids, Lake N. Stensjön, in subsequent years. All fish belong to the 1954 year-class. Note that slow-growing fish were caught at higher age (LEE's phenomenon).

Sample	n.	I	II	III	IV	V	VI	VII	VIII	IX	N. Stensjön
1955	17	157	(208)	—	—	—	—	—	—	—	—
1956	116	151	262	(317)	—	—	—	—	—	—	—
1957	71	148	255	329	(383)	—	—	—	—	—	—
1958	108	146	249	323	387	(419)	—	—	—	—	—
1959	81	147	250	322	384	423	(443)	—	—	—	—
1960	47	155	256	321	384	423	447	(463)	—	—	—
1961	14	144	251	323	383	424	446	464	(476)	—	—
1962	11	150	259	331	396	435	462	480	493	(498)	—
1963	8	138	245	317	377	418	445	464	478	485	(485)
Average	473	149	254	324	385	423	448	469	486	485	—

430 F2 fish. The average was very nearly the same (29.3 and 29.1) respectively. According to general Mendelian principles the distribution of gillrakers should be broader in the F2 than in F1. This was also true; the spectrum of variation being 21—39 and 21—36 respectively. A X^2 test on the gillraker distribution difference of F1 and F2 gave a P of less than 0.001. A considerable genetical unbalance, therefore, of the more extreme F2 fish does not seriously affect their viability. The net fertility of the F1 generation must thus be said to be good.

In Lakes S. Stensjön and Öratjärn (Table 3) the introduced F2 hybrids (of the cross whitefish × cisco) could by natural spawning produce an F3 generation. Again, the F2 could be separated from the F3 by means of scale-reading, since all the introduced fish were of the same year-class.

Again, the average gillraker number is roughly the same (36.4, 36.9). If all the F2 fish had the same power of reproducing themselves, the distribution of gillrakers would have been the same in the two generations. However, this was by no means the case. The variation is much broader in the F2 than in the F3 generation. The difference is, as tested by X^2, highly significant. The most extreme fish, having most unbalanced genomes, were thus not capable of reproducing themselves as were the fish with more balanced genomes. The fertility of the F2 generation is therefore reduced, though still fairly good (Fig. 1).

A more direct piece of evidence would be to introduce hybrids along with parent species, or F1 along with F2 fish, in the same environment and let them prove their relative fertility in comparison. There are, however, practical difficulties in organizing such an experiment. One is the heterosis effect and another is the problem of assigning the fish to either category. The indirect evidence now at hand has demonstrated that the lower fertility of some hybrid fish will certainly work as a selection against hybrids in nature.

It might here be added, that chromosome irregularities seem to prevail

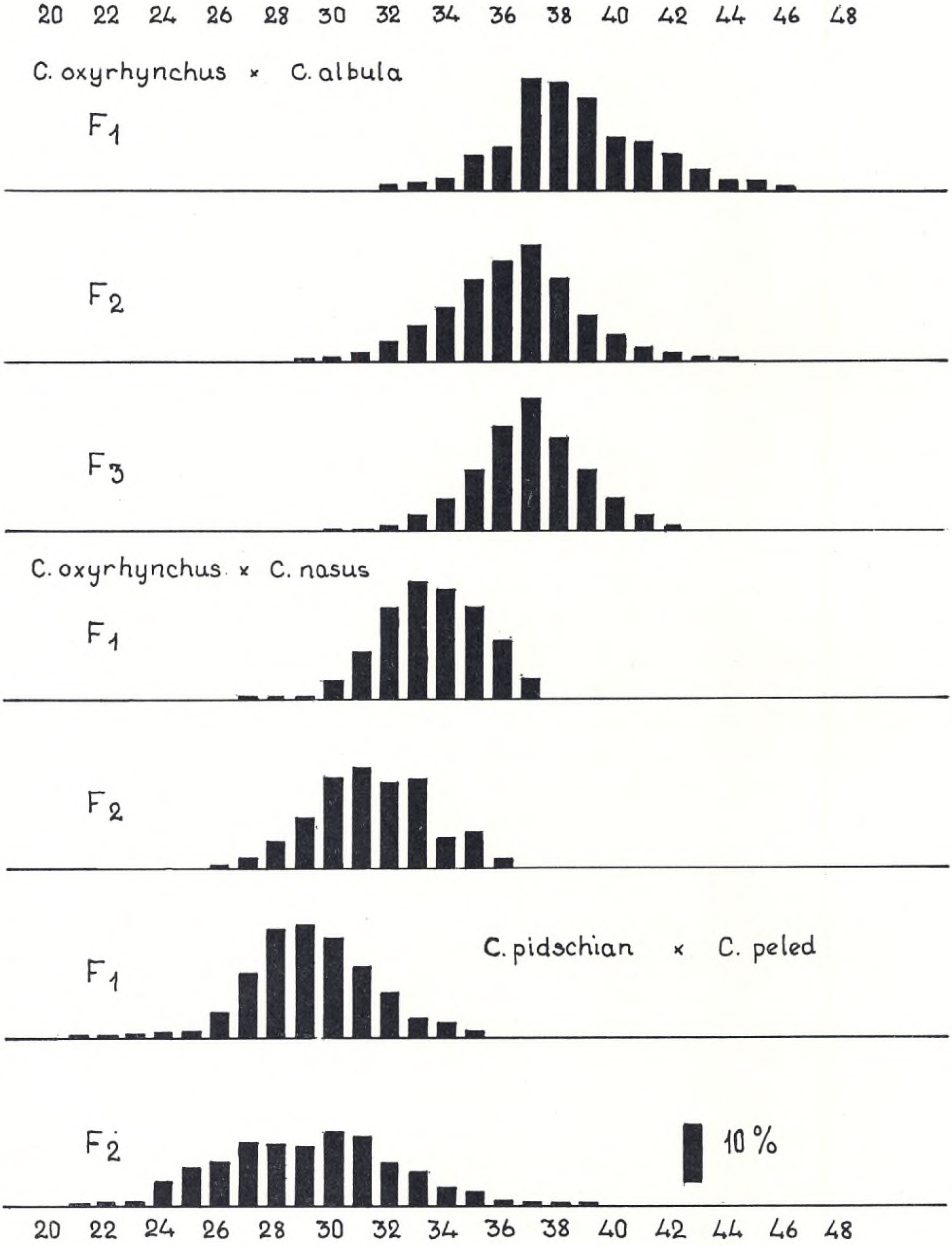


Fig. 1. The gillraker distribution of hybrid whitefish. There is a tendency for fewer gillrakers in F_2 than in F_1. The variation is broader in F_2. The lower fertility of the F_2 gives a reduced variation in F_3.

Table 9. Growth (total length in mm) as calculated from scales of F2 hybrids, Lake S. Stensjön, in subsequent years. All fish belong to the 1958 year-class.

Sample	n.	I	II	III	IV	V	VI	VII	VIII	IX
1959	121	118	(214)	—	—	—	—	—	—	—
1960	105	113	225	(267)	—	—	—	—	—	—
1961	110	93	220	267	(290)	—	—	—	—	—
1962	95	93	218	265	291	(306)	—	—	—	—
1963	57	92	218	264	290	307	(321)	—	—	—
1964	10	103	227	267	292	308	324	(341)	—	—
Average	498	103	221	266	291	307	324	—	—	—

in many whitefish populations (Svärdson 1945, Kupka 1948, 1950, Karbe 1964 a). It is suggestive to find this correlation between chromosome studies and the reduced fertility of unbalanced hybrid genomes in a group of species where introgression is of evolutionary importance.

The correlation age (growth) — number of gillrakers. It was shown earlier that the full adult number of gillrakers was not achieved when the fingerlings were 70 mm long (Svärdson 1950) but that this — in two ponds — was true when the fingerlings were of 100—120 mm total length (Svärdson 1952 p. 218). Later Lindroth (1957) found that the rakers were first visible as small knots at a fish length of 20 mm and had the definite number at 100 mm total fish length. Lindström (1962) proved the gradual increase of rakers in the fry and the possibility to identify three species when 80—100 mm total length. The *pidschian* fingerlings in Table 7 provide further evidence.

Apart from this ontogenetic phenomenon there is also a slight increase of gillrakers in adult fish of different ages, the older fish having more rakers. This is an apparent change, probably due to sampling errors and the selective power of fishing. The evidence comes from the sampling in subsequent years of one single year-class, in Lakes N. Stensjön, S. Stensjön and Öratjärn (Tables 3 and 4).

The combined samples from N. Stensjön in 1955—58, compared with the samples 1959—63 comprise 235 and 165 fish respectively, all hatched in the spring of 1954. The average gillraker numbers are 29.03 and 29.79 respectively. The difference is highly significant ($P < 0.0005$).

The sample from Öratjärn 1960 compared with the samples 1961—64 comprise 142 fish and 124 respectively, all hatched in the spring of 1957. The average gillraker numbers are 35.99 and 36.94 respectively. The difference is highly significant ($P < 0.0005$).

The samples from S. Stensjön 1960—61 compared with the samples 1962—64 comprise 201 and 166 fish respectively, all hatched in the spring of 1958. The average gillraker number are 35.99 and 36.72 respectively. The difference is significant ($P = 0.005$).

Table 10. Growth (total length in mm) as calculated from scales of F2 hybrids, Lake Öratjärn, in subsequent samples. All fish belong to the 1957 year-class.

Sample	n.	I	II	III	IV	V	VI	VII	VIII	IX
1960	149	94	191	252	(285)	—	—	—	—	—
1961	75	82	188	249	289	(311)	—	—	—	—
1962	44	86	191	255	296	321	(340)	—	—	—
1963	2	77	199	256	299	325	356	(390)	—	—
1964	3	83	185	252	294	317	341	369	(391)	—
Average	273	89	190	252	292	321	347	369	—	—

The very same tendency has been found also in other experiments where fish in tarns have been sampled in subsequent years. The reality of the phenomenon cannot be doubted.

There is a broad general correlation between growth rate and gillrakers, when different populations are studied (SVÄRDSON 1952). Even within a population, an individual correlation may occur. To test this possibility the growth data of the whitefish from N. Stensjön, S. Stensjön and Öratjärn are given (Tables 9 and 10). The back calculation from the annuli on the scales was performed by the routine method used by the Institute. The Lee phenomenon is obvious, indicating that in all lakes the fastest growing fish (with fewer rakers) have been caught predominantly in their early life while the slightly slower-growing fish (with more gillrakers) have been left for capture in later years, i.e. when the fish are older. The environmental plasticity of growth is, however, also demonstrated in the material: the growth of the same F2 generation in Lakes S. Stensjön and Öratjärn is rather different. At four years of age both groups have the same length. But in Lake S. Stensjön growth is rapid during the first years, and then is inferior to that of Lake Öratjärn. When these growth data are WALFORD-plotted, the K is 0.65 for S. Stensjön and 0.36 for Öratjärn.

The growth rate is correlated with the diet of the fish. As a rule the more bottom forms that are eaten, the faster the whitefish will grow. The diet of the *pidschian* and the *peled* has been studied in Lake Vojmsjön (NILSSON 1958) and in the lakes Storavan—Uddjaur (NILSSON 1960, LINDSTRÖM and NILSSON 1962). *Pidschian* is mainly a bottom feeder while *peled* is a plankton feeder (Lake Vojmsjön) or a surface feeder (Uddjaur—Storavan).

The diet of the hybrids *pidschian*×*peled* in Lake N. Stensjön was studied in 1964 (Table 11). The fish have been divided into two groups, those having 22—28 gillrakers and those having 29—36. In Lake N. Stensjön the hybrids feed on the bottom fauna and plankton and are thus intermediate between their parent species. There is a slight tendency for the fish with more gillrakers to have fed on a more pronounced pelagic diet. They have taken more *Bosmina, Daphnia* and *Holopedium* and less *Eurycercus* than have

Table 11. Stomach contents (as percentage of the total in those filled) of hybrid whitefish from Lake N. Stensjön in 1964. The general diet is intermediate between that of the parent species. Fish with more gillrakers have a slight tendency to a more pelagic diet.

	22—28 gillrakers		29—36 gillrakers	
	August	September	August	September
Bosmina	—	—	3.2	—
Bythotrephes	11.8	12.7	9.5	16.1
Daphnia	—	—	2.2	—
Eurycercus	23.1	35.4	20.3	16.5
Holopedium	26.2	16.4	31.5	27.8
Lymnæa	—	4.8	—	—
Planorbis	—	6.9	—	—
Pisidium	1.0	0.2	0.4	—
Chironomidae l	—	3.4	6.5	0.2
Dytiscidae l	+	—	1.0	—
Trichoptera	—	—	—	4.4
Chironomidae p	15.1	10.6	11.1	9.5
Trichoptera p	—	—	0.4	—
Hydrachniidae	+	0.7	0.2	—
Terrestr. insects	1.6	5.9	0.6	16.0
Insect-remains	0.3	—	0.4	1.3
Plankton-remains	20.6	3.0	6.3	—
Ephippium	—	—	—	6.6
Plants, stones	0.3	—	0.1	1.6
Algae (*Nostac.*)	—	—	6.3	—
Filled stomachs	23	10	22	11
Empty stomachs	10	2	4	—

the fish with few gillrakers. In September they have fed on terrestrial insects like their *peled* parent.

The conclusion of this section is that within a hybrid whitefish population the food habits and growth rates may differ slightly between fish with a low or a high number of gillrakers. Since fish with more gillrakers tend to roam about more pelagically, they grow slightly slower and are not caught so easily in bottom-standing gill nets along the shore as are fish with fewer rakers. Therefore, fish with more rakers tend to predominate among fish that are not caught until of higher age. When the rakers of subsequent samples are considered, fish of low age will tend to have fewer rakers than fish of higher age.

Gillraker genetics. »The number of gillrakers has, in principle, nothing to do with the question of how the whitefish forms should be understood» (SVÄRDSON 1952, p. 229). Nevertheless they are of the utmost importance since they constitute the only morphological character so far proved not to be considerably modified by environment. The genetical basis of their num-

Fig. 2. Spawning whitefish from the mouth of the river Indalsälven. Bergeforsen, November 1964.

Fig. 3. Spawning whitefish of the same stock, raised in a montain lake. Note the deeper bodies and darker backs in this environment. Lake Kölsjön, October 1964.

ber is proved by transplantations, artificial selection experiments and their intermediate number in species hybrids. They therefore serve as genetical markers of populations. This importance is still more strengthened by the finding (last section) that their number is correlated to tendencies of diet and growth dissimilarities.

In the first analysis (Svärdson 1952) there were possibilities open for environmental modifications of some 1—2 rakers. Since then, however, there have been two findings that give raise to doubt whether any environmental modification does occur. The result of artificial selection in one natural population was two progenies with widely different gillraker averages (33.8 and 38.3 respectively from a mother population of 36.0). (Svärdson p. 312 1957 a.) Therefore, the *founder principle* must be taken in account when transplantations have been made. The thirty *C. clupeaformis* reared all their lives in captivity by Koelz (Lindsey 1962, 1963) had some 2—3 rakers less than the parent stock. This may, however, have been the result of unintentional selection of some extreme parent fish when the eggs were stripped and fertilized. In other transplantations of few fish or eggs (Svärdson 1952) the genes of the parent stock may not have been adequately sampled.

In Table 1 the transplantation of 185,000 eyed eggs of the Baltic whitefish to Lake Kölsjön is reported (cf. Figs. 2 and 3). Since 1948 no certain change of the gillrakers has occurred. It is true that the average of the fish taken in 1958 is low. If this had been the only sample available from Lake Kölsjön a nongenetical modification would have been suggested. The 1958 sample is aberrant. It may be due to the performance of an un-trained technical assistant or, what is more probable, be the result of the age effect in sampling. There were many young fish in this year's sample (60 out of 114 fish were II+).

When the founder principle and the age effect are considered, therefore, there is *no evidence up to now that gillrakers have been modified in numbers by environment*. Natural selection has not, in the first 15 years, changed the gillrakers of the Baltic whitefish transplanted to the quite different habitat of Lake Kölsjön. In natural populations the selection may tend to keep the gillraker number constant for long periods. Samples from Svärdson 1957 a (p. 343) and Table 2 illustrate this principle:

Lake Bullaren 1873	33.1
Lake Bullaren 1954	32.9
Lake Ringsjön 1872—1882	37.2
Lake Ringsjön 1952	37.5
Lake St. Skeppträsket 1913	40.0
Lake St. Skeppträsket 1964	40.1

The result of artificial selection and the rakers in hybrids indicate that the number of gillrakers is determined by numerous genes. In three cases the gillrakers of the F1 generation can be compared to that of the F2 generation:

F1	F2	Difference	Details in Table
38.6	36.4	2.2	3
33.5	31.4	2.1	2
29.3	29.1	0.2	4

In all cases there is a drop in the average from F1 to F2. In two cases the reproduction of F1 was interfered with by man. The founder principle, therefore, may have been involved. However, there are two lakes and one tarn behind the 36.4 value for F2 in the upper line. Sub-samples of eggs were stripped in two different years. Yet, the averages are 36.4, 36.4 and 36.3 (cf. Table 3). This indicates that the unintentional selection of atypical parent fish is probably not the whole explanation.

If the drop in gillraker numbers from F1 to F2 is real, it might indicate that higher numbers of gillrakers are produced by more raker genes being added to the genome of the population. The principal difference between F1 and F2 is mainly that the parental chromosomes are still maintained in the F1 but are recombined by crossing over in the F2. The genetical unbalance is greater in F2. If more raker genes are involved in producing 38 rakers than in producing 29, the effect of unbalance and misfunction of the genes would reduce the gillrakers more in the 38-fish than the 29-fish. This seems to be the case.

Thus a third source of error is introduced into the problem of sampling whitefish for gillraker studies. A genetically more unbalanced sample may have fewer rakers and be wrongly interpreted as environmentally modified.

At present the genetics of the gillrakers is mostly speculative. But it must be argued that the gillrakers are so far the most suitable markers of whitefish populations, giving generalized information about the genetic status of the population concerned.

The premating isolating mechanisms. MAYR (1964) discussed the premating isolating mechanisms under three categories:

a. seasonal and habitat selection
b. ethological isolation
c. mechanical isolation.

There is, of course, no mechanical hindrance for fertilization in whitefish. The spawning was described by FABRICIUS and LINDROTH (1954) and the main features of the spawning are complete promiscuity and no fighting, nipping, chasing, threatening, or other aggressive behaviour. »Actually, the whitefish seem to be the most peaceful species of fish we have ever watched» (*op.cit.*). Fish that have just spawned in the free water may snap up their own sinking eggs, and immature fish, or those of another whitefish species, may join the spawning group to feed on the eggs. Partners in incomplete spawning acts could be of the same sex as well as of opposite sexes. Even single specimens, males or females, could perform rushes towards the surface as when spawning. The spawning takes place in the evening, almost at dark. It is practically certain that a ripe fish of a sympatric whitefish species, feeding on eggs or otherwise being at the spawning place, may have a very good chance of producing interspecific hybrids. The ethological isolation must be said to be extremely poor.

More effective is the seasonal and habitat isolation (SVÄRDSON 1949). Apart from the great bodies of water, like the Baltic, Lake Vänern, Lake Vättern and Lake Ladoga, the adult size of sympatric whitefish species is most often different. Size segregation is the basis for the fishermen's keen eye on specific differences. Sympatric species usually have different names, given to them by the local population.

This size and seasonal isolation is illustrated by the material from the Gimå River lakes (Tables 5—7):

Stability of spawning periods. The spawning period of whitefish is fixed by the proximate factors, light-sensitivity (photoperiod) and water temperature. The photoperiodism would tend to keep the species isolated. Water temperature, however, may be fluctuating, locally as well as annually. FABRICIUS (1950) pointed out that *C. pidschian* spawned in different months in various parts of Lake Vojmsjön, and SVÄRDSON (1953) that *C. lavaretus* spawned 2—3 weeks earlier than average in the cold autumn of 1952, and that the spawning season is as long as 35—50 days in this population of Lake Idsjön.

When the Bure river whitefish were transplanted from the Baltic to the lakes in the parish of Malå there was no change of spawning time (October) while the native whitefish species spawned in December—January (SVÄRDSON 1951). When, however, *C. lavaretus* from Lake Idsjön was transplanted to Lakes Öjingen and Målingen in the Ljusnan river system the spawning period was unchanged in Lake Öjingen but changed from October to January—February in Lake Målingen. The whitefish in Lake Kölsjön spawn somewhat earlier than the parent stock in the Indalsälven river.

The isolation of whitefish species by their spawning seasons is therefore no doubt of a certain albeit limited effect. Local and annual fluctuations in water temperature may influence the spawning and some males may be ripe months in advance of the females of the same species.

Size segregation. It seems somewhat paradoxical that size segregation is the dominant premating mechanism, keeping the sympatric whitefish species genetically isolated. Size, of course, depends on growth rate, the span of life, and the pressure of interspecific competition. Though there is a genetically based tendency for diet preferences, growth rate and span of life, all are exceptionally modified by environment, as transplantations have demonstrated. In fact, it has been known from practical experience since the 18th

Table 12. Age distribution and maximum size of *C. lavaretus,* sampled 1947—1963 in the spawning run from Lake Idsjön into the mouth of the Gimå river.

Sample	I+	II+	III+	IV+	V+	VI+	VII+	VIII+	Largest fish in cm	n
1947	—	6	27	9	3	2	1	—	(37.5)	48
1948	—	3	81	12	1	—	—	—	(34.5)	97
1949	—	—	101	233	8	—	—	1	(37.0)	343
1950	1	—	4	35	23	—	—	—	(29.0)	63
1951	—	—	43	94	32	30	1	—	(37.5)	200
1952	—	—	27	56	40	24	3	—	(30.5)	150
1953	—	—	42	131	82	23	17	4	(32.5)	299
1954	—	1	22	189	55	26	2	—	(32.0)	295
1955	—	—	49	161	59	19	8	2	(36.5)	298
1956	—	—	209	69	15	4	—	1	(32.0)	298
1957	—	—	27	253	9	6	3	—	(32.5)	298
1958	—	—	60	161	76	3	1	1	(31.0)	302
1959	—	—	9	169	95	27	2	1	(34.0)	303
1960	—	—	21	75	168	31	7	—	(31.0)	302
1961	—	33	82	68	105	20	4	—	(30.0)	312
1962	—	110	67	63	73	3	1	—	(28.0)	317
1963	—	4	224	45	25	2	—	—	(30.5)	300

Total number of aged fish: 4,225

century that even dwarfed whitefish may grow to large fish if transplanted to lakes, that are rich in food and without whitefish. It is also known that the very first generations of an introduced population may have an excellent growth rate, while growth will later deteriorate and, finally, the population might again be more or less dwarfed (OLOFSSON 1932, SVÄRDSON 1949, 1950, 1951). Dwarfs of low average age may also, when transplanted, have their lives lengthened to almost twice the normal span of life (SVÄRDSON 1951, p. 121).

Highly significant for the understanding of the size segregation is the phenomenon of »*intra-lake transplantation*». This means that fish of one species join the schools of another and adopt *all the size characteristics of the latter*. The physiological effect is just the same as if the fish were transplanted by man to another physical environment, that is to say another lake.

In Lake Idsjön *lavaretus* is medium-sized, *pidschian* is large and *nasus* is a dwarf. In Table 5 all the samples, taken in the spawning periods of the species are given in detail. It can be seen that there are some *lavaretus* specimens appearing in the samples of *pidschian,* as well as *nasus*. They could be egg predators, present only temporarily at the spawning grounds, or »transplanted» fish.

In order to separate these two categories of foreign fish, the growth data were considered. In Table 12 are given the ages of more than 4,000 spawning *lavaretus,* which is part of the parallel population study. The maximum fish size for each year is also given. All these fish were not identified on their gillrakers. The samples of fish for gillraker investigation are given in Table 5.

It is supposed, however, that all 4,000 fish were pure *lavaretus,* as judged by their age and size.

Egg-predating *lavaretus* among the spawning *pidschian* have been marked in Table 5 as ( ). They were identified as egg predators if their age and size was normal for *lavaretus.* These fish fell out as exceptions:

Sample	Gillrakers	Age	Total length, cm
Dec. 56	33	VI+	36.5
Jan. 57	33	XII+	53.0
»	35	XIII+	44.0
Dec. 58	33	X+	37.0
»	38	XII+	43.0
Dec. 60	37	XIII+	36.5
Dec. 61	33	XV+	47.0
Dec. 63	31	IX+	41.0

These exceptional fish are too old and too large for *lavaretus,* but their gillrakers prove them to be of that species. Some few may be hybrids but since these should have fewer gillrakers, like the fish with 26—29 gillrakers in Table 5, they are probably pure *lavaretus* but »transplanted» within the lake. To judge from their scales they have probably lived with the *pidschian* since their first or second year. Their span of life is almost twice the normal *lavaretus* value.

In Table 5 there are also some *lavaretus* caught among the dwarfed *nasus.* Most of these *lavaretus* are egg predators or stray individuals. One fish of 32 gillrakers, one with 33 and one with 34 are, however, to judge from their scales, dwarfs from the very start of their lives. They are dwarfed *lavaretus* or, possibly, hybrids.

In Lake Locknesjön (Table 7) some foreign fish were probably egg-predators only, and in Lake Ansjön (Table 6) growth is so similar and introgression so advanced that it is not possible to separate egg predators from »transplanted» fish. The phenomenon of »intra-lake transplantation» is widespread and is found in almost every lake where intensive studies have been made. The first case was reported from Lake Storsjön in the province of Härjedalen (SVÄRDSON 1951, p. 115).

The schooling is generally interpreted as being based on optical stimuli. Whatever its base, its effect must be extremely strong, since fish of a foreign species may be »school-trapped» for many years. In fact, they might be incorporated into the school almost as effectively as if they lived in another lake. The sympatric species of whitefish may be said to live in »lakes of their own», though they all swim around in a rather small lake, sometimes feeding on the other species' eggs and in summer often being caught in the same set of gill nets. The physiological basis of this extreme school tenacity ought to be studied. It is suggestive that whitefish have a smell, that is easily perceived even by humans. There is no information, that different whitefish species smell different to the human nose. LINNAEUS, however, found that the smaller of two sympatric *Osmerus* species had a stronger smell.

Ants are known to recognize the members of the nest society by smell. If the diet of an individual whitefish modifies its smell, any stray whitefish fry or fingerlings, that happened to get mixed up with another species' school, would adopt the other species' smell and afterwards tend to keep contact with the adopting species. Some sort of chemical imprinting may be involved.

LINDSTRÖM (1962) caught fry of two whitefish species in the very same hauls of a small seine. He points out that the fry possibly did not swim in one school but certainly occurred in the same habitat at the very same time.

The school tenacity of the whitefish has been discussed before. STEINMANN (1950) thought it to be strong enough to make possible an ecological isolation, resulting in the sympatric evolution of new species. It is nowadays well known that this is impossible, but it does function as the strongest premating mechanism of isolation in keeping the whitefish species apart. The *pidschian* of Lake Idsjön proves, however, that this kind of isolation is broken by a few fish almost every year.

The postmating isolating mechanisms. MAYR (1964) lists the following categories of postmating mechanisms:

a. Gametic mortality
b. Zygote mortality
c. Hybrid inviability
d. Hybrid sterility

In the group of sibling whitefish species the postmating isolating mechanisms are poorly evolved. There is no gametic mortality or zygote mortality, and the viability of the F1 hybrid is *increased* by some 10—20 per cent compared to the parent species.

Only the fourth of the barriers listed above is working. As shown in an earlier section, the F1 fertility is good while that of the F2 generation is somewhat reduced. Possibly also the backcrossings give fewer offspring than the F1 generation.

When lakes with sympatric whitefish species are studied in some detail, hybrids or probable hybrid fish are often found. The evidence for hybrids, however, depends on the possibilities of identifying the hybrids, e.g. the distribution of gillrakers in the parent species. In Lake Idsjön, hybrids between *nasus* and *pidschian* cannot be identified, whereas hybrids between *lavaretus* and the other two species can. Table 5 includes some fish, caught among the *pidschian,* which, as judging by their gillrakers, are hybrids.

In Lake Locknesjön (Table 7) the possibilities of identifying hybrids are greater. There are two fish with 31 and 32 rakers, caught in February 1957 and January 1956 respectively, which are certain hybrids.

The most abundant species within a lake is also the most effectively isolated. Any stray foreign fish, included by the school tenacity in the population of a less abundant species, implies a good chance of hybridization and, hence, a genetical disturbance in the next generation. The net fertility of the rarer species will then be somewhat reduced. This involves further threat to the integrity of the species; the rarer it becomes, the more dangerous is the influx of fish of the sympatric species.

This accelerating process of genetical parasitism by the most abundant species on the less abundant is illustrated by Lake Ansjön (Table 6), where *pidschian* and *nasus* are almost gone and *lavaretus* is highly introgressed by *oxyrhynchus*. This species is the one most likely to exist, as sole survivor, in the lake in the future. 300 fish taken without selection, and before spawning periods, in October 1964 with nets of different mesh sizes, gave predominantly *oxyrhynchus* fish.

It is a general experience that the large-sized *pidschian* is the rarest species all over Sweden and the one most sensitive to fishing, water regulation and disturbances in natural balance, e.g. by the practice of releasing newly hatched fry of unknown species. This practice was started in Sweden in the 1860s (WIDEGREN 1870).

In 1964 experiments were started to introduce *pidschian* fingerlings (from Lake Locknesjön) into Lake Ansjön in order to test whether the species could be brought back by man to be of some importance in the lake's balance as well as in the fishery. At the same time the frequency of future hybrids could be roughly estimated.

It is logical that euthrophication of a lake should change the former balance between several sympatric whitefish species (KARBE 1964) and that a change in predator or fishing pressure should have similar effects (SMITH 1964).

It is interesting to speculate on the tendency to dwarfing (cf. FENDERSON 1964) of *Coregonus* as an evolved reaction of survival value in sympatric occurrence. If large fish are always most severely genetically parasitized, then the tendency to facultative dwarfing would be favoured by natural selection.

IV. The whitefish species concept

It has been pointed out that the sympatric whitefish populations should be ranked as species (SVÄRDSON 1949). They do not conform at all to the subspecies concept, except that they may interbreed freely in some cases. However, such cases are rather advanced cases of introgression and preliminaries to complete extermination (by genetical parasitism) by one species of another. Much more common are cases where there is some slight gene flow, causing a gradual evolution of converging morphological traits.

The taxonomy of a group of sibling species like the *Coregonus*-complex cannot be treated by the morphological »type concept». Since nobody at present knows which population is most or least introgressed, a gradual work of "restoration" of probable postglacial invaders must be built up. Most urgent at present is to find some other morphological character, being as firmly based genetically as the gillrakers, but also suitable for statistical treatments of whole populations.

From an evolutionary point of view the ineffective isolating mechanisms of the *Coregonus* sibling species is of interest. Though the survival premium of better isolation is high, and the selection has thus been intense during the postglacial period of some 10,000 years, the mechanisms are still based on non-genetical modifications like growth tendencies, size segregation, school tenacity and rather plastic spawning periods. The fertility of the hybrids is modestly reduced by genetical unbalance. Wherever the same ineffective barriers exist, the result would be a group of fish, split up in »biological fractions», »ecological races», »spawning groups» or displaying »evolutionary instability» or »intense speciation». They illustrate the most important evolutionary step, i.e. that from isolated population up to the level of species.

Summary

1. One transplantation and four hybridization experiments involving sympatric whitefish species are described. The hybrids have been raised to F1, F2 or, in one case, to the F3 generation.
2. Three neighbouring lakes within the Gimå river system have been studied by numerous whitefish samples for more than a decade. The gillraker distribution of the samples, taken during the spawning period of the species, is given.
3. The viability of hybrid fish is not reduced. On the contrary they demonstrate hybrid vigour and some 10—20 per cent better survival than a parent species when grown under the same environmental conditions.
4. There is some reduction of the F2 fertility but little, if any, reduction of the fertility of the F1 generation. This could be demonstrated by reduced variability of the F3 fish compared to the F2 generation.
5. Subsequent samples of one year-class give slightly higher averages of gillraker counts. This is correlated to growth, the fish with more rakers having slightly inferior growth rate and thus dominating among the older fish. More pelagic habitat selection and more dominant planktonic diet are probable parallel trends.

6. The number of gillrakers is based on polygenes. There is some evidence that more rakers are produced by the adding to the genome of further raker genes. F1 tend to have more gillrakers than the subsequent F2 generation of hybrids.
7. The premating isolating mechanisms are discussed. They are rather ineffective, based partly on non-genetical modifications. Size segregation, extreme school tenacity and tendencies to different growth rates are most important.
8. Postmating isolating mechanisms are also ineffective. Unbalanced hybrids are selected against. An abundant species may genetically parasitize the less abundant sympatric ones and gradually undermine its net fertility in comparison with the competing species. There is a general tendency for a large-sized, less abundant species, like *C. pidschian* to be threatened by extermination. The facultative dwarfing of most *Coregonus* species may have been evolved as a consequence of this genetical parasitism.

References

DOTTRENS, E. 1959. Systématique des Corégones de l'Europe occidentale, basé sur une étude biometrique. *Rev. Suisse Zool. 66: 1—66.*

FABRICIUS, E. 1950. Heterogenous stimulus summation in the release of spawning activities in fish. *Rept. Inst. Freshw. Res. Drottningholm: 31: 57—99.*

— and A. LINDROTH, 1954. Experimental observations on the spawning of whitefish, *Coregonus lavaretus* L. in the stream Aquarium of the Hölle Laboratory at River Indalsälven. *Rept. Inst. Freshw. Res. Drottningholm 35: 105—112.*

FENDERSON, O. C. 1964. Evidence of subpopulations of Lake Whitefish, *Coregonus clupeaformis,* involving a dwarfed form. *Trans. Amer. Fish. Soc. 93 (1): 77—94.*

GARSIDE, E. T. and F. E. J. FRY, 1959. A possible relationship between yolk size and differentiation in trout embryos. *Can. J. Zool. Vol. 37: 383—386.*

— and W. J. CHRISTIE. 1962. Experimental hybridization among three Coregonine fishes. *Trans. Amer. Fish. Soc. 91 (2): 196—200.*

GASOWSKA, MATYLDA, 1958. The morphology of hybrids and the ways of inheriting parental features by reciprocal hybrids: whitefish × small whitefish (*Coregonus lavaretus maraenoides* POLJAKOW × *C. albula* L.) *Polskie Archiwum Hydrobiol. Tom IV (XVII): 277—287.*

— 1960. Genus *Coregonus* L. discussed in connection with a new systematic feature that of shape and proportion of *os maxillare* and *os supramaxillare. Polska Akad. Nauk Annales Zoologici XVIII (26): 471—514.*

KARBE, L. 1964 a. Die Chromosomenverhältnisse bei den Coregonen des Bodensees und einiger weiterer voralpiner Seen, ein Beitrag zum Problem der Speziation in der Gattung *Coregonus. Zeitschr. zool. Syst. Evol. Bd 2: 18—40.*

— 1964 b. Die Auswirkung der künstlichen Eutrophierung des Bodensees auf das Artgefüge seiner Coregonenpopulationen. *Mitt. Hamb. Zool. Mus. Inst. Kosswig-Festschrift: 83—90.*

KUPKA, E. 1948. Chromosomale Verschiedenheiten bei schweizerischen Coregonen. *Rev. Suisse Zool. 55: 285—293.*

— 1950. Die Mitosen- und Chromosomenverhältnisse bei der grossen Schweberenke, *Coregonus wartmanni* (BLOCH) des Attersees. *Öster. zool. Z. 2: 605—623.*

LINDROTH, A. 1957. A study of the whitefish (*Coregonus*) of the Sundsvall Bay District. *Rept. Inst. Freshw. Res. Drottningholm 38: 70—108.*

LINDSAY, C. C. 1962. Distinctions between the broad whitefish, *Coregonus nasus,* and other North American whitefishes. *J. Fish. Res. Bd. Canada, 19 (4): 687—714.*

— 1963. Sympatric occurrence of two species of Humpback Whitefish in Squanga Lake, Yukon Territory. *J. Fish. Res. Bd. Canada 20 (3): 749—767.*

LINDSTRÖM, TH. 1962. Life history of whitefish young (Coregonus) in two lake reservoirs. *Rept. Inst. Freshw. Res. Drottningholm 44: 113—144.*

— and N.-A. NILSSON. 1962. On the competiton between whitefish species. In E. D. LECREN and M. W. HOLDGATE, Ed. *The Exploitation of natural animal populations* (BLACKWELL Sci. Publ. Oxford): *326—340.*

MAYR, E. 1964. *Animal species and evolution. Harvard Univ. Press. 798 pp.*

MELANDER, Y. and E. MONTÉN, 1950. Probable parthenogenesis in *Coregonus. Hereditas* XXXVI: 20.

MOENKHAUS, J. 1910. Cross fertilization among fishes. *Proc. Indiana Acad. Sci.: 353—393.*

NILSSON, N.-A. 1958. On the food competition between two species of *Coregonus* in a North Swedish lake. *Rept. Inst. Freshw. Res. Drottningholm 39: 146—161.*

— 1960. Seasonal fluctuations in the food segregation of Trout, Char and Whitefish in 14 North-Swedish lakes. *Rept. Inst. Freshw. Res. Drottningholm 41: 185—205.*

OLOFSSON, O. Några inplanteringar av Lomsjösik. *Svensk Fiskeritidskrift 43: 4—8, 16—18, 43—47, 74—79.*

RESHETNIKOV, Y. S. 1963. Ob ismenchivosti sigov (*Coregonus* variability) *Zoologichesky Zhurnal, Tom XLI, Vyp 8: 1187—1199.*

SMITH, S. H. 1964. Status of the deepwater Cisco population of Lake Michigan. *Trans. Amer. Fish. Soc. 93 (2): 155—163.*

STEINMANN, P. 1950. Monographie der schweizerischen Koregonen. *Schweiz. Z. Hydrol. 12 and 13.*

SVÄRDSON, G. 1945. Chromosome studies on Salmonidae. *Rept. Inst. Freshw. Res. Drottningholm 23: 1—151.*

— 1949. The Coregonid Problem. I. Some general aspects of the problem. *Rept. Inst. Freshw. Res. Drottningholm. 29: 89—101.*

— 1950. The Coregonid Problem. II. Morphology of two Coregonid species in differents environments. *Rept. Inst. Freshw. Research, Drottningholm 31: 151—162.*

— 1951. The Coregonid Problem. III. Whitefish from the Baltic, successfully introduced into fresh water in the North of Sweden. *Rept. Inst. Freshwater Research, Drottningholm 32: 79—125.*

— 1952. The Coregonid Problem. IV. The significance of scales and gillrakers. *Rept. Inst. Freshw. Res. Drottningholm 33: 204—232.*

— 1953. The Coregonid Problem. V. Sympatric whitefish species of Lakes Idsjön, Storsjön and Hornavan. *Rept. Inst. Freshw. Res. Drottningholm 34: 141—166.*

— 1957 a. The Coregonid Problem. VI. The Palearctic species and their intergrades. *Rept. Inst. Freshw. Res. Drottningholm 38: 267—356.*

— 1957 b. Skeppträsklöjan. *Svensk Fiskeritidskrift 66: 37—42.*

— 1958. Interspecific hybrid populations in Coregonus. *Uppsala Universitets Årsskrift 6: 231—239.*

— 1959. Sikarna i Locknesjön. *Svensk Fiskeritidskrift 68: 137—139.*

— 1961. Young sibling fish species in northwestern Europe. *In* W. F. BLAIR, ed. *Vertebrate speciation (Univ. Texas Press): 498—513.*

WIDEGREN, HJ. 1870. Fiskeriintendentens årsberättelser för år 1868. *Kongl. Svenska Landtbruks-Akademiens Handlingar Vol. 28 (1870): 3—68.*

Char and Whitefish Recruitment in North Swedish Lake Reservoirs

By THOROLF LINDSTRÖM

Introduction

BEVERTON and HOLT (1957) define the age at recruitment as the age at which fish enter the area where fishing is in progress, that is, at which they become liable to "encounters" with the gear, *cf. op.cit.* pp. 28, 30 and 244. RICKER (1958) defines recruitment as the addition of new fish to the vulnerable population by growth from among smaller size categories and HOLT (1960) gives a symbol, *R,* defined as the number of fish entering the exploitable phase of a stock in a given period.

The more our knowledge of fish young habitats in freshwater increases, the more possible it appears to adopt a definition according to BEVERTON and HOLT (1957) for freshwater species, too. This is of primary importance for an analysis of the influence of the immature and mature stock size on the mortality of the young of the same species (RICKER 1954, p. 608). For the time being, the more neutral definitions of RICKER (1958) and HOLT (1960) are, however, more appropriate for many freshwater situations.

Earlier in recruitment research history, it was generally assumed that fish young passed a short critical stage when mortality was very high, and that a study of the environment should reveal the mortality factor when the time for the critical stage was well established. It is thus logical that research on char recruitment in Scandinavian lake reservoirs of storage type should in the forties centre around the relationship between year-class abundance and the amplitude of the winter draw-down of the reservoir level, i.e. drainage during a season when the year-class occurred as eggs and fry. When no relationship was found, this was sometimes taken to indicate that recruitment in the reservoir was essentially undamaged.

The cognizance of methodical difficulties has subsequently increased as it has been revealed that:

(1) the fish populations are drastically redistributed both in spawning time and in other parts of the life cycle when a lake is transformed into a reservoir (FABRICIUS 1950, LINDSTRÖM 1954, AASS 1960 a & b, NILSSON 1961, RUNNSTRÖM 1963). As running water and the pelagical zone are involved in the redistribution, as well as the littoral zone, it is necessary to match density indices from different kinds of gears (cf. TAYLOR, 1958),

(2) aging of char scales is more difficult than it was earlier thought to be (NORDENG 1961),

(3) there are growth changes in the populations (RUNNSTRÖM 1964 a), which make it necessary to know more about the efficiency and selection properties of gill nets of different mesh sizes, when indices of year-class abundance are to be calculated from gill net catches,
(4) a lake reservoir is in a way a habitat totally different from the lake from which it has arisen. The possibility of using catch per unit effort as an index of comparative abundance if sampling is repeated during similar conditions (RUSSEL 1931), so important to ordinary population analysis, may not exist during a transitory phase when a lake is converted into a reservoir,
(5) whereas the advance of whitefish systematics have kept pace with that of reservoir studies, a corresponding study of char systematics has lagged behind.

The material brought together in reservoir studies has to serve several purposes and can seldom meet the increased demand for completeness and diversification arousing from the complications listed. As the confidence felt in the obtained year-class abundance indices has decreased, a number of models on the recruitment in reservoirs have been developed from the increasing knowledge of the environmental changes in the reservoirs and the life history of whitefish and char young in reservoirs and natural lakes. Since both approaches have their obvious merits and drawbacks, the inferential evidence is presented in the following pages, succeeded by the direct attempts at year-class abundance estimates.

1. Recruitment models for reservoirs from inferential evidence

The models in this chapter concern mainly lake reservoirs of storage type. Details about lake-level management are given in Section 3.

A general trend in recruitment studies from different fields as reported by SIMPSON (1956) and RICKER (1958, pp. 231—236) is that several mortality factors are assumed to be working over a comparatively long period. A single factor must have a considerable effect if it is to show up with significance in a correlation study (BEVERTON and HOLT 1957, p. 275, RICKER 1958, p. 234) where several factors are involved. There are some cases where one factor seems to have been very important, but for a recruitment study in a new case it is safe to include several factors in the hypotheses, and a factor such as winter drainage amplitude may of course influence recruitment in different ways simultaneously. Since environment and fish populations are different in reservoirs that have different purposes and with different lake-level managements, hypotheses should correspondingly be different, and experiences from Scandinavian regions have thus an exceptionally high value for the present study.

From behaviour studies on spawning char and whitefish (FABRICIUS 1953, FABRICIUS and GUSTAFSON 1954, FABRICIUS and LINDROTH 1954) and from lake surveys published in Fishery Board memoranda (in Swedish, mimeo-

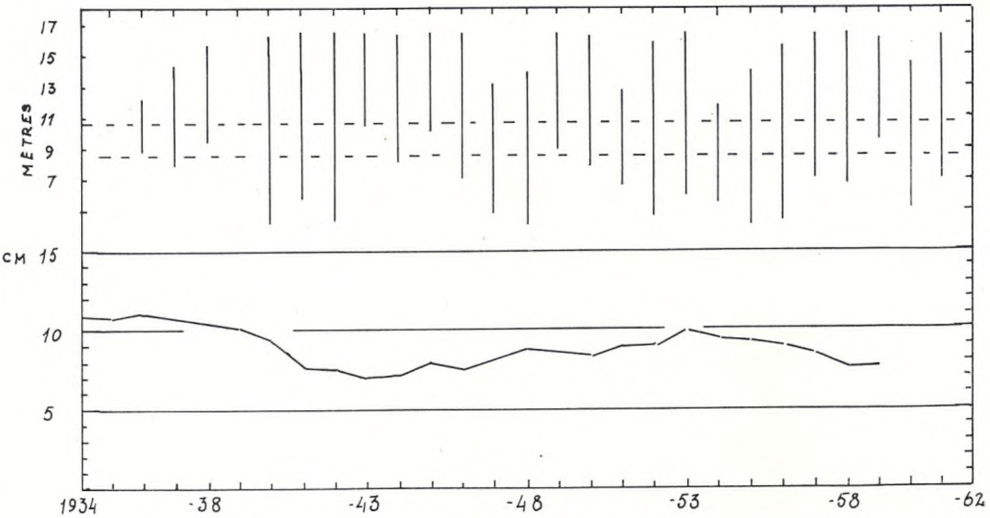


Fig. 1. Total length of one-year-old char in Lake Torrön according to RUNNSTRÖM, back-calculated material, and lake-level variations in the different years (local system). The lake was converted into a storage lake reservoir in 1936. Mean high-water and low-water levels before that year are indicated with broken lines.

graphed) there emerges a good deal of knowledge about the spacing of the eggs and the spawning sites and digging behaviour of the parents, i.e. the habitats of the eggs. Next comes information about hatching time, food, growth and habitat for the whitefish young (SVÄRDSON 1949—1957, LINDROTH 1957, LINDSTRÖM 1962) and information about hatching time, growth and some additional data from the life history of the char eggs and char young in Scandinavia (RUNNSTRÖM 1951, AASS 1964). This material forms the framework for the following models.

The damming-up phase

RUNNSTRÖM (1964 a) has studied growth during the whole life of char and whitefish on back-calculated scale material. He concludes that there is a pulse of good growth during the first years of a storage lake reservoir if the management includes damming over the old lake level, and he terms this the damming-up phase. He shows that this good growth is followed by a strong downward trend in the growth. The difficulties of aging char scales do not greatly influence this study, and though char growth data may be attributed to the wrong calender year, the general trend of a growth pulse as presented by RUNNSTRÖM is a real one. RUNNSTRÖM concludes that "for a limited time the feebler rate of growth can even be increased because of the fact that good nutritive conditions during the first years of impoundment can give rise to rich year classes".

Table 1. Total length of one-year-old whitefish from Lake Kallsjön, Jämtland, "back-calculated" from the scales of older fish. The whitefish, *C. nasus,* was introduced in the twenties and there is probably a growth trend connected with the population expansion. From 1941 to 1945 the amplitude of the lake-level management was kept between the natural mean high-water and mean low-water level but from 1946 the amplitude was increased by a further one metre and new land was inundated.

		Total length, mean of all material from year-class:			
		1934—40	1941—45	1946—48	1949—55
Age at capture	II+	—	93	128	114
	III+	126	127	117	105
	IV+	159	105	118	107
	V+	133	108	114	103
	VI+	141	100	108	105
	VII+	151	97	123	105
	VIII+	102	109	109	111
	IX+	—	115	109	106
Mean of the means III+—VIII+		135	108	115	106
Total number		19	213	521	499

Thus according to this interpretation both a general good growth and some rich year-classes arise during the first years of certain lake reservoirs, but there is a further complication: the growth during the first year of life of these year-classes does not contribute to the general picture of good growth during the damming-up phase so far as char is concerned. One-year-old char does not show any better growth during the damming-up phase and their growth in the reservoir is on average not so good as in the natural lake, as is shown by Fig. 1, reproduced from a mimeographed report by Runnström. Inundated new land around Lake Storavan may have produced a slight improvement in the growth of whitefish young, according to studies by the present author (1962, p. 139). This difference between char and whitefish receives further confirmation through the back-calculated first-year length of whitefish from Lake Kallsjön, Table 1, made available to me by Dr G. Svärdson. The whitefish young may use the rich food animal supply from the flooded marshes in a dammed-up lake (Nilsson 1964) more than char young, judged by the littoral occurrence of whitefish young in Lakes Storavan and Uddjaur and by the behaviour of char young reported by Frost (1963—64).

In spite of the strong dependence of survival on growth during the first year of life usually (Ricker and Foerster 1948), there is no satisfactory *a priori* hypothesis regarding the connections between growth and survival during the transitional years of conversion of a lake into a lake reservoir, as the predators are still unknown, as are also their reactions to the conversion of the lake. The good supply of food of different kinds during the damming-up phase may divert the interest of facultative predators from the char and whitefish young; or, contrariwise, the behaviour of the young in the new environment may contribute to an increased pressure from the predators, resulting in increased and decreased survival, respectively, of slow-growing young.

The year-class 1946 is dominating in all the samples from Lake Kallsjön in the catch years 1949—1952.

RUNNSTRÖM's hypothesis that rich year-classes arise during the damming-up phase is thus substantiated mainly by the general good supply of invertebrate fish prey as "animals from the surroundings" and zooplankton, according to GRIMÅS (1962, 1965 a and b), NILSSON (1961, 1964) and AXELSON (1961), and so far as whitefish is concerned by the age composition of the analysed samples from Lake Kallsjön. In the present context the case will be developed only a little further. Inferential evidence published by the present author (1955) makes it improbable that plankton crustacea form the main food of char young in some lakes during their first spring, and food studies on whitefish young by the present author (1962) show that they are certainly not solely dependent on plankton food during their first year, feeding also on *Diptera,* mainly chironomids, hymenopters and hemipteres, mainly *Aphididae,* all of small size.

The effect of severe winter drainage on survival of char

AASS (1960 a and b) has shown that the char recruitment is cut down in the reservoir Lake Pålsbufjord, a reservoir with a normal winter drainage of 22 metres. He reports an abundance of small char, two years old (and thus possible to age) resulting from a spawning-hatching winter with exceptionally little drainage, only 12 metres. This shows that the amplitude of winter drainage also should be included in a recruitment model, but this part of the model cannot yet be attributed exclusively to any of the two phases in reservoir history.

The draw-down phase

This term, like "the damming-up phase" has been coined by NILSSON (1964) and RUNNSTRÖM (1964 a). The draw-down phase includes long-term trends in storage lake reservoirs. Among those trends, the decrease in bottom animals (STUBE 1958, AASS 1960, GRIMÅS 1961, 1962, 1964, 1965 a) and certain cladocerean species (LÖTMARKER 1964) should enter among the plausible biological relationships that are important for recruitment. A detailed analysis of the feeding habits of the young and the changes in food fauna composition is, however, still lacking, and so far as the cladoceres are concerned the conclusion is somewhat dubious, as LÖTMARKER states that the decreased standing crop might result *inter alia* from increased fish grazing.

Otherwise the decrease in food animal populations is likely to affect the number of char and whitefish that can grow fast enough to escape predators during a critical period (RICKER and FOERSTER 1948, LINDSTRÖM and NILSSON 1962, LINDSTRÖM 1962, p. 141).

The growth of char young during their first year is slower in the reservoir than in a natural lake, as reported, but it is difficult to judge the long-term trend in growth of whitefish young from the material in Table 1, as the whitefish *Coregonus nasus,* PALLAS, was introduced into Lake Kallsjön in the twenties and the population is still expanding according to RUNNSTRÖM, Fishery Board memorandum of September 13, 1958. If there is one long-term growth trend effected by the population expansion and another effected by the reservoir conversion, they must be difficult to separate.

An important element is missing here, too, for the combination of the model, *viz.* a knowledge of the predators and the changes in their populations; consequently it is difficult to make use in the model of any observed growth changes in char or whitefish young. This concerns the recruitment of char and whitefish in natural lakes, too. Whitefish population control in natural lakes in Sweden has been treated by SVÄRDSON (1957, 1962). He develops further the theory of the RICKER and FOERSTER model referred to above and particularly emphasizes the temperature in early summer, as giving whitefish young good growth; he also stresses the size of the adult whitefish population, interfering with the whitefish young population through food competition or cannibalism.

The parent—progeny relationship has recently been discussed by RICKER (1954, 1958), BEVERTON and HOLT (1957), GULLAND (1962) and BEVERTON (1962). BEVERTON and HOLT show that a decreasing right limb in the recruitment curve can occur with the model of RICKER and FOERSTER without cannibalism or food competition on the part of the adult population being involved, as of course a decreasing right limb can be achieved with cannibalism and food competition from the adults without introduction of the RICKER and FOERSTER model. BEVERTON and HOLT also show that the population is self-compensating only if certain conditions are fulfilled when the mathematical representation of the model is that given on p. 56 (*op.cit.*), and they state that an asymptotic recruitment curve is probably the most generally useful at the present time. It can, however, be assumed that the mathematical representation of the RICKER and FOERSTER model given by BEVERTON and HOLT on pp. 56—57 should be further elaborated in order to show the possibilities of the model, e.g. by introducing facultative predators, turning to other prey at a certain fish-young density, and other egg-production curves, but there is at present no reproduction curve published for Swedish whitefish or char populations that could have substantiated further analysis (Cf. CHRISTIE, 1963).

2. Estimates of fish-young abundance during their first year of life

The estimation of whitefish-young abundance in shallow water has proved to be technically difficult, as already discussed by the author (1962). The efforts ended in establishing important habitats for whitefish young. The habitat of char young in Scandinavia is not very well known.

3. Estimates of the abundance of young fish more than one year old but not yet catchable by the gear ordinarily used in the lake

In these studies there are some sources of error that are certainly very relevant, e.g. the lack of studies on fish density in the pelagial region of the lakes and the incomplete taxonomic study of the whitefish and char in the catches — there is often a pelagial whitefish reported or suspected in the North Swedish lakes. There is no good check on fish migrating into or out from the lakes studied.

Lake Kultsjön was slightly influenced after 1954 through the impoundment of Lake Ransaren higher up in the same river, the influence concerning lake-level variations and turbidity. In the winter of 1958/59 Lake Kultsjön was transformed into a storage lake reservoir with an annual lake-level rhythm shown i Fig. 2. The amplitude of the lake-level regulation is about 5 metres and the level is allowed to rise 3 dm above the old normal high-water level; consequently a damming-up phase, though not a very significant one, is to be expected. Water is stored in the summer and released in the winter. The fish fauna is mainly a char-burbot population with some trout as well. For further information about the lake, cf. RODHE (1964), NILSSON (1964), RUNNSTRÖM (1964 a).

The studies concern the years 1954—62 (LINDSTRÖM and NILSSON 1964), but fishing was not standardized until 1958, when it was concentrated at three stations where two sets of nine gill nets, each with seven different mesh sizes, were set from the shore and along the bottom, fishing both in shallow and fairly deep water (some 15 metres). This fishing technique reduces the possibility of studying variations between stations along the shore, but of course gives more information about the variation in a vertical direction. Both kinds of variation are analysed, and as a consequence a correction — not numerically specified — should be applied to the values for Nassjoviken, Fig. 3, reducing the downward trend somewhat. The complete material of small-meshed gill nets consists of some 2,100 efforts (one net, one night).

The catch of char per unit effort with small-meshed gill nets dropped during the years 1958—62 while other changes are inconsistent. The burbot population is, however, not yet thoroughly studied. The char material is condensed in Fig. 3. The drop in char catch may reflect a change in the catching abilities of the gill nets in the sometimes rather turbid water or a

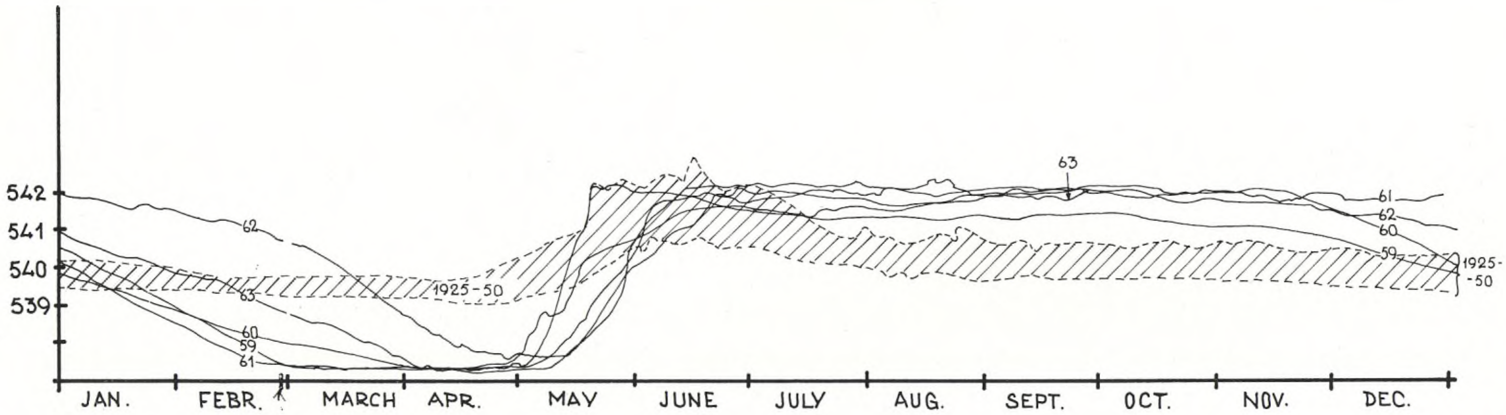


Fig. 2. Latitude of variation in natural lake level in Lake Kultsjön in the years 1925—1950, obliquely hatched, and lake-level variations during 1959—1963. The old normal high-water level was 541.94; below the extreme high values of the hatched area, but not always surmounted by the 1959—1963 water levels in the summer and autumn. The variations in the years 1955—58 fell almost entirely within the hatched area.

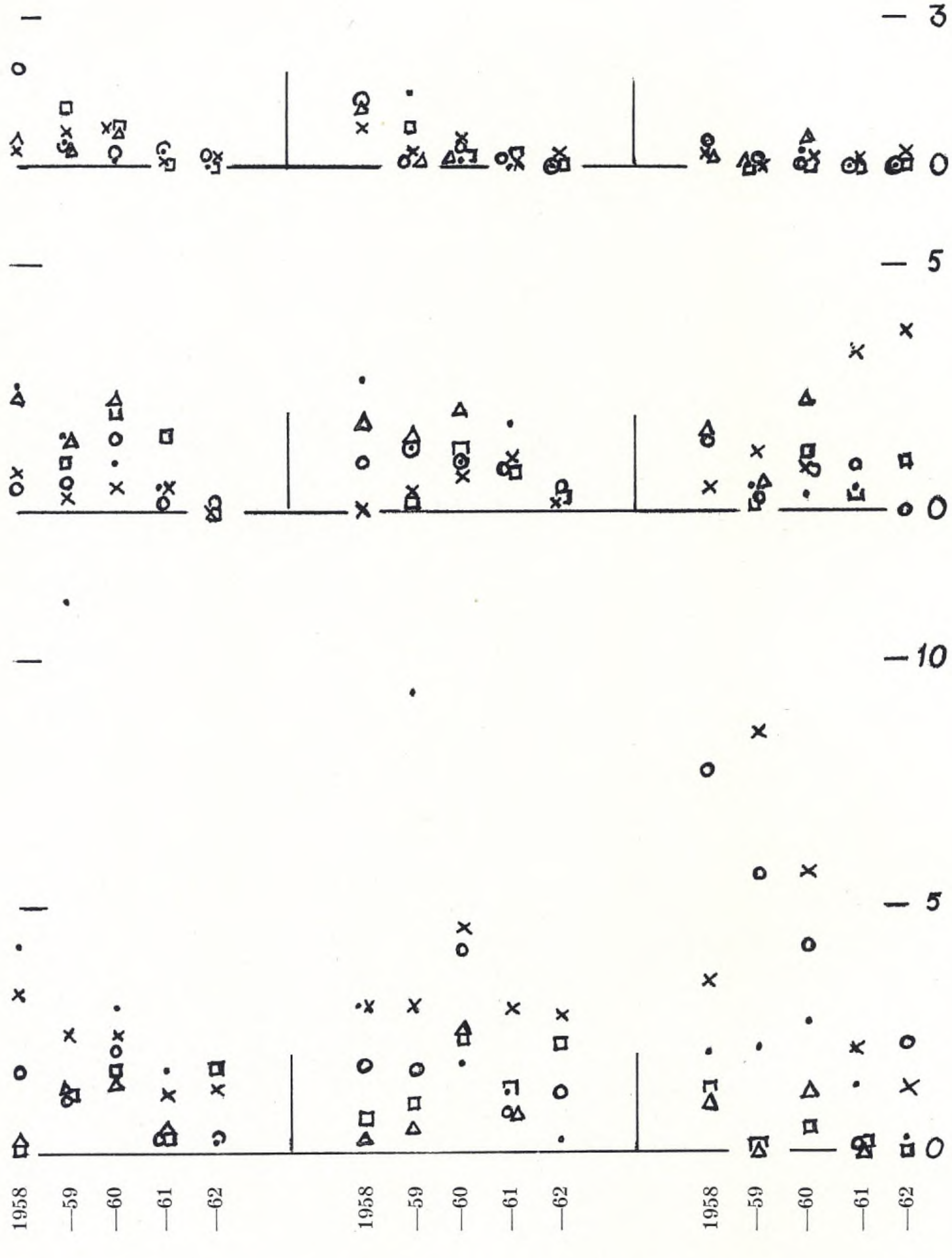


Fig. 3. Lake Kultsjön, catch of char in number per unit effort. There are three localities, Prästnäset above, Saxnäs in the middle and Nassjoviken at the bottom. There are three gill-net categories, 2.50 knot-to-knot bar measure on the left, 2.14 in the middle and 1.67 on the right. Catch year indicated at the bottom of the figure. June, July, August, September and October are indicated with dots, crosses, circles, triangles and squares respectively.

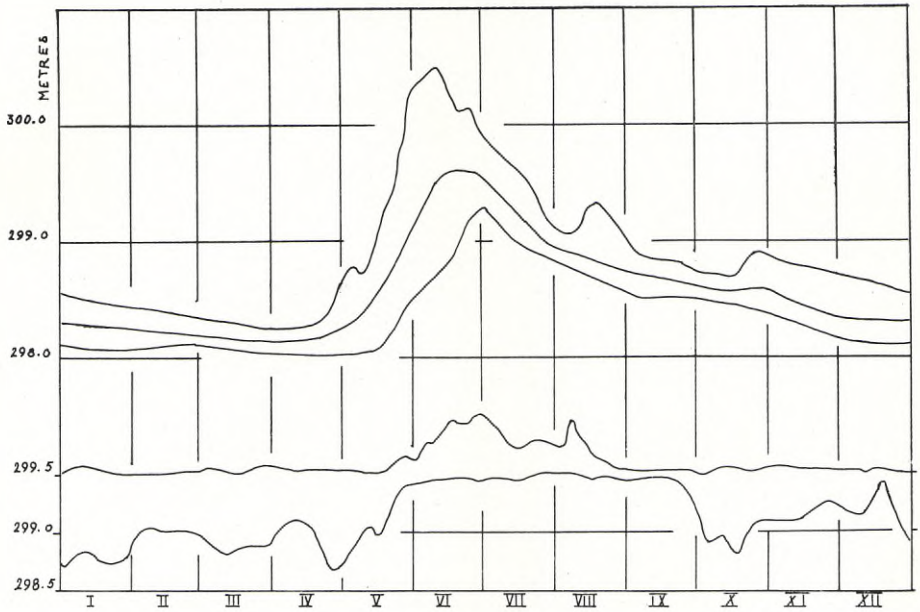


Fig. 4. Lake Barselet, range of natural lake-level variations and normal water level in 1949—57 at the top, regulated lake-level variation range in 1958—64 at the bottom.

shifting of the centre of small-char habitat from the old one towards a more pelagial region — by this latter expression the authors meant any part of the lake that cannot be fished with bottom-set gill nets, 5 ft high — or it may reflect a real drop in char recruitment as an effect of the conversion into a lake reservoir. According to the analysis of variance, the differences between years are of low significance and because of methodological difficulties (NORDENG 1961) age analyses have not been performed; but the drop is shown in three different mesh-size categories, 2.50, 2.14 and 1.67 cm knot-to-knot bar measure. A choice between the hypotheses will probably be easier when other students of Lake Kultsjön have published their material (cf. GRIMÅS 1965 b).

Lake Barselet was a "sel" in the River Ume älv, i.e. the flow was (and is) great compared to the volume of the lake. The lake has been affected by dam constructions, channel digging and power-plant constructions in the river above Lake Barselet. The turbidity may have increased slightly after the spring fishing 1955 (Table 2), but it was aggravated later on, particularly in 1958. The yearly fluctuations in the lake-level are much slighter in Barselet than in the reservoirs of storage type. The fluctuations after 1957 were affected both through lake-level regulations at the power-plant dam at the outlet of Barselet and through a storage reservoir higher up in the river. The total effect is illustrated by Fig. 4, showing that the yearly lake-level ampli-

Table 2. Number of whitefish per unit effort in gill nets.

Knot-to-knot bar measure, cm	Catch year	Section:								
		I	II	III	IV	V	VI	VII	VIII	$\bar{x}_{I-VIII}$
						Spring				
2.14	1955	2.0	2.5	1.5	3.5	1.0	1.0	1.5	1.0	1.8
	56	5.7	4.0	1.7	2.3	1.3	2.3	6.7	4.7	3.6
	57	5.3	1.7	1.7	1.7	0.3	0.7	2.0	11.0	3.0
	58	4.0	2.3	1.0	10.7	5.0	6.7	8.0	18.0	7.0
	59	5.0	2.5	—	4.7	2.0	1.3	4.0	4.0	—
	61	1.0	2.5	—	12.8	4.0	2.9	2.2	1.8	—
	64	—	—	—	—	—	—	—	—	—
	$\bar{x}_{55-58}$	4.3	2.6	1.5	4.6	1.9	2.7	4.6	8.7	—
1.67	1955	0.5	0.5	0	2.0	0	0	9.0	2.5	1.8
	56	6.3	1.7	1.3	0	0.7	0.3	5.0	2.3	2.2
	57	3.3	2.7	1.7	1.0	1.7	1.3	3.3	37.5	5.5
	58	16.7	3.3	1.3	11.0	4.0	16.0	19.7	17.0	11.1
	59	12.0	4.5	—	2.7	2.5	3.0	6.0	13.3	—
	$\bar{x}_{55-58}$	6.7	2.1	1.1	3.5	1.6	4.4	9.3	14.8	—
						Autumn				
2.14	1955	1.0	7.5	0.5	0	1.3	2.5	3.0	3.5	2.4
	56	16.0	9.3	10.7	3.3	5.7	3.7	7.3	11.0	8.4
	57	9.7	4.3	9.0	3.7	8.0	8.3	5.0	8.5	7.1
	58	1.0	2.3	2.3	0.7	1.7	3.0	8.3	4.5	3.0
	59	10.0	13.0	—	13.5	—	8.0	6.0	9.0	—
	61	9.0	7.5	—	—	6.5	11.0	5.4	15.7	—
	64	12.8	5.5	—	—	—	—	8.3	12.8	—
	$\bar{x}_{55-58}$	6.9	5.9	5.6	1.9	4.2	4.4	5.9	6.9	—
1.67	1955	2.0	13.0	2.5	5.5	6.0	2.5	12.5	17.0	7.6
	56	18.0	5.3	10.0	3.3	1.0	8.7	12.3	10.3	8.6
	57	11.3	5.0	12.7	5.0	2.7	4.3	7.0	9.5	7.2
	58	6.3	1.7	5.0	2.0	4.3	1.7	15.7	8.0	5.6
	59	18.5	10.0	—	5.5	—	—	3.0	5.0	—
	$\bar{x}_{55-58}$	9.4	6.3	7.6	4.0	3.5	4.3	11.9	11.2	—

tude now is smaller. There is a short-term lake-level management between September and May included (diel or weekly rhythms). The flow is now more uniform throughout the year. The yield from Barselet consists to about 50 % of whitefish and furthermore of pike, perch, grayling, trout and burbot.

The studies started in 1955, mainly with sets of gill nets of the same composition as in Lake Kultsjön, but the sets were broken up into groups of three nets, and these groups were set starting from the shoreline. The lake is divided into 8 sections, and because of the high intraclass variation the differences between sections as regards the number of whitefish per unit effort do not stand out so significantly in an analysis of variance as did the differences between stations in Lake Kultsjön. The ordinary fishing in Lake Barsele does not take whitefish in the size categories characteristic of gill nets with 2.14 and 1.67 cm knot-to-knot bar measure, so the catches in these nets were chosen as indices of year-class abundance in Table 2. The material consists of some 400 efforts with such nets.

At least two whitefish species are involved. Year-classes 1953—57 show retarded growth. At an age of three years the length of the different whitefish species was similar and so was the length at this age in 1955 and 1964 (year-classes 1952 and 1961). Thus the gill nets with 2.14 bar measure 1955 and 1964 are appropriate for a comparison of year-classes, as these nets in the autumn caught fish of ages II+, III+ and IV+; but neither these nets nor the other data given in Table 2 lend support to the idea that the catch of these age classes decreased after the conversion of the lake into a power-plant reservoir.

The serious turbidity in 1958 seems to have influenced the autumn catch in that year, according to Table 2. The 1959 year-class cannot be estimated; but, if the recruitment was damaged, the population recovered later. There are vague indications published in the complete account by the present author (1964) that the recruitment in Lake Barselet was fortified from whitefish populations in the adjacent lakes from 1958. Any reasonable hypothesis concerning the abundance of young whitefish in the central and unfished part of Lake Barselet would say that, when the conversion of the lake began, both newcomers and native young whitefish would shun the central part with its turbid flow and search the protected parts along the shores. The increased turbidity is now fading away, so the accomplished comparison of catches in small-meshed gill nets should really tell us something about the population, but the lack of fishing in the pelagial zone is a serious drawback in this as in other reservoir studies.

4. Estimates of recruitment from estimates of the abundance of fish in exploited size categories

In these studies new sources of error are added to those listed earlier. The local fishermen often maintain that the char and whitefish fishery has been damaged, e.g. some years after a lake is converted into a storage lake reservoir; but good figures for the total yield are difficult to obtain. It is thus ordinarily not possible to account for any change in the yield when indices of year-class abundance are estimated from catches of adult fish in biological surveys.

In the following studies of two storage lake reservoirs, the authors have not given much credence to actual figures for total yield, but from a good knowledge of the fishery they have considered a correction for changes in total yield to be unnecessary when computing estimates of year-class abundance.

In the winter of 1953/54 Lake Limingen in Norway was converted into a storage lake reservoir. The amplitude of the lake-level regulation is about 6 metres and the annual rhythm similar to that of Lake Kultsjön (Fig. 2). New land is not inundated. One estimate gives char as 85 % of the yield, trout as 15 %. The study was performed by Aass (1963) and concerns the

Table 3. Mean number of char caught per net and individual mean weight of the char in a set of gill nets presented in the text. AASS 1963.

	Mean number, summer fishing	Mean number, char spawning fishing	Mean weight summer fishing, grammes	Mean weight char spawning fishing, grammes
1953	0.8	2.3	332	289
1954	0.9	2.7	339	245
1955	0.6	2.4	310	253
1956	0.6	1.9	300	244
1957	0.8	3.1	285	230
1958	0.9	2.8	277	241
1959	1.0	3.3	260	228
1960	0.8	3.6	301	225
1961	1.0	3.5	255	217

years 1953—61. The lake was netted during the summer and during char spawning with a set of gill nets with six different mesh sizes ranging between 2.5 and 4.3 cm knot-to-knot bar measure. The nets with the two medium mesh sizes numbered three in each set, the four remaining categories being represented by only one in each set. Summer fishing was carried out on 200 stations along the shoreline (lake area 95 square kilometres), char spawning fishing was carried out on 7—9 spawning areas. Table 3 shows the mean number of char per net and individual mean weight of char caught in the set.

According to AASS many processes have contributed to this result, e.g. changes in growth and condition of fish, variation in mean age of the catchable stock and possibly changes in the year-class abundance. There may also have been a drop in the total yield and a rise in the catching ability of the gill nets in spawning fishing, both overemphasizing the impression of a gradual increase of the char stock in number. Age analysis of the char is not presented. In summarizing, AASS states that the recruitment of char was unchanged or possibly somewhat higher after the conversion of the lake into a reservoir.

RUNNSTRÖM (1964 b) has studied a spawning migration of char to the inlet area of Lake Jormsjön, a lake reservoir of storage type. The amplitude of the lake-level regulation is about 4 metres, starting from 1949, the annual rhythm is similar to that of Lake Kultsjön, (Fig. 2) and the lake level is allowed to rise about 1/2 metre above the natural normal high-water level. An insignificant damming-up phase could be expected, followed by a drawdown phase after some few years. The studies were carried out in the period 1947—59 and in all about 152,000 char were checked by netting the lake immediately below the inlet and by controlling fish in traps in a weir across the lower part of the main tributary, both regions containing spawning sites for the char. Char constitutes about 2/3rd of the total yield from the lake, the remaining yield being trout.

Table 4. Indices of year-class abundance for char in Lake Jormsjön, according to RUNNSTRÖM (1964 b). Lake conversion in 1949.

1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956
—41.3	+5.8	+28.6	+6.5	—5.5	—86.8	—40.1	+9.3	—6.3	+70.5	+67.7

From marking in the lake part of the spawning area and recaptures of ascending char in the weir traps, RUNNSTRÖM gets a raising factor of PETERSEN type to raise the trap catch to a total for the entire spawning stock in the inlet area. Aging of samples from the trap catches was carried out on scales, and the results applied to the totals for the spawning stock of the inlet area each year. Starting from the small recoveries in the spawning control of char marked in preceding spawning migrations, RUNNSTRÖM argues that for the relevant estimates it is possible to neglect the source of error in reading scales of old char (after the scale growth has ceased, NORDENG 1961), as the char in Lake Jormsjön do not seem to live very long.

RUNNSTRÖM presents some material showing that the inlet spawning area is of dominating importance for the char stock of Lake Jormsjön after the conversion of the lake into a lake reservoir. Assuming that this situation was essentially not affected by the conversion from a natural lake and that the total yield from the lake is too small to invalidate his conclusions (these assumptions are not explicit but are otherwise evident from his text), RUNNSTRÖM concludes that the year-class analysis of the spawning stock from the inlet area shows that the conversion into a lake reservoir has not affected the year-class abundance for this population. The indices of year-class abundance are presented in Table 4.

RUNNSTRÖM's Table 14 shows that the modal age at spawning has dropped from the age of 5 to the age of 4 summers; this observation is not discussed but it should have some bearings on the year-class discussion too. A drop in the mean age of the catchable char stock is also reported by AASS from Lake Limingen. In a natural lake it would have indicated an increase in the fishing, but as the recruitment may have changed when a lake is converted into a lake reservoir one can only conclude that the relationship between recruitment and the post-recruitment mortality is disturbed. If the yield has not increased in number, the recruitment might have decreased, or the natural mortality might have increased. AASS (1963), who discusses the point, assumes that the natural mortality of old char has increased.

5. A tentative summary

The recruitment models for storage lake reservoirs ("impounded lakes") in Section 1 and the recruitment estimates in sections 3 and 4, Lakes Kultsjön, Limingen and Jormsjön are not altogether consistent.

The damming-up phases of Lakes Kultsjön and Jormsjön were perhaps too insignificant to produce any rich year-classes. Rich year-classes of char in Lakes Kultsjön and Jormsjön may of course also have arisen as a consequence of the damming-up without being revealed by the sampling methods. With the evidence at present available there is, however, reason to look for differences between the whitefish and char populations in their reactions to a damming-up phase. The model is then only applicable to whitefish young and the habitat choice of char young not only excludes them from the growth-promoting food supply from overflowed marshes (p. 127) but also from other advantageous features in the damming-up phase.

According to the model, the recruitment of char in the draw-down phase in Lakes Limingen and Jormsjön should decrease, but the estimates based on the abundance of fish in exploited size categories do not follow the prediction. New kinds of evidence are needed.

A so far undamaged recruitment of whitefish in Lake Barselet has not been predicted by any model, as studies in power-plant reservoirs ("river reservoirs") are of more recent origin, but such a result is quite consistent with the good nutritive conditions reported by GRIMÅS and NILSSON (1965) and the rich supply of zooplankton reported by LÖTMARKER (verbal communication) from other power-plant reservoirs. In the sheltered and more littoral habitats of Barselet there are at least some requisites for rich plankton populations.

If there is a need for a more concise appraisal of the effect of the conversion of a Swedish lake into a reservoir — which is undoubtedly the case — one has to evaluate the sources of error that are involved in the three approaches, i.e. life-history studies (the models), estimates of young-fish abundance and estimates of abundance of exploited size categories, and this is the reason for the ample discussion of sources of errors in the present paper.

Acknowledgements

The help of the late Mr D. ALEXANDERSSON, who processed part of the fishery data from Lakes Kultsjön and Barselet, is gratefully acknowledged, as is also the assistance in scale reading given by Mrs BIRGITTA LINDHOLM, Mrs INGER NORDAHL and Mr LENNART ERIKSSON.

References

AASS, P. 1960 a. The effects of impoundment on inland fisheries. *IUCN seventh technical meeting. Vol. IV: 69—76.*

— 1960 b. Vassdragsreguleringene og fisket. *Insp. for ferskvannsfiskets vitenskaplige avdeling.* Mimeographed. In Norwegian.

— 1963. Limningenreguleringens virkninger på fisket. Mimeographed memorandum. In Norwegian.

— 1964. Reguleringer og røyerekruttering. *Jakt, fiske, friluftsliv (9): 378—381.* In Norwegian.

AXELSON, J. 1961. Zooplankton and impoundment of two lakes in Northern Sweden. *Rep. Inst. Freshw. Res. Drottningholm 42: 84—168.*

BEVERTON, R. J. H. and S. J. HOLT. 1957. On the dynamics of exploited fish populations. *Fish. Invest. Lond. Ser. II, 19: 1—533.*

BEVERTON, R. J. H. 1962. Long-term dynamics of certain North Sea fish populations. *Brit. Ecol. Soc. Symposium II, editors Le Cren & Holdgate: 242—259.*

CHRISTIE, W. J. 1963. Effects of artificial propagation and the weather on recruitment in the Lake Ontario Whitefish fishery. *J. Fish. Res. Bd. Canada, 20: 597—646.*

FABRICIUS, E. 1950. Heterogeneous stimulus summation in the release of spawning activities in fish. *Rep. Inst. Freshw. Res. Drottningholm 31: 57—99.*

— 1953. Aquarium observations on the spawning behaviour of the char, *Salmo alpinus. Rep. Inst. Freshw. Res. Drottningholm 34: 14—48.*

— and K.-J. GUSTAFSON. 1954. Further aquarium observations on the spawning behaviour of the char, *Salmo alpinus. Rept. Inst. Freshw. Res. Drottningholm 35: 58—104.*

— and A. LINDROTH. 1954. Experimental observations on the spawning of whitefish, *Coregonus lavaretus,* in the stream aquarium of the Hölle laboratory at River Indalsälven. *Rep. Inst. Freshw. Res. Drottningholm 35: 105—112.*

FROST, WINNIFRED. 1963—64. In Director's report. *Freshwater Biological Ass., Annual Rep. 31: 32—33 and 32: 36—37.*

GRIMÅS, U. 1961. The bottom fauna of natural and impounded lakes in northern Sweden (Ankarvattnet and Blåsjön). *Rep. Inst. Freshw. Res. Drottningholm 42: 183—237.*

— 1962. The effect of increased water level fluctuation upon the bottom fauna in Lake Blåsjön, northern Sweden. *Rep. Inst. Freshw. Res. Drottningholm 44: 14—41.*

— 1964. Studies on the bottom fauna of impounded lakes in southern Norway. *Rep. Inst. Freshw. Res. Drottningholm 45: 94—104.*

— 1965 a. Effects of impoundment on the bottom fauna of high mountain lakes. *Acta Universitatis Upsaliensis. Abstracts of Uppsala Dissertations in Science 51: 1—24.*

— 1965 b. The short-term effect of artificial water-level fluctuations upon the littoral fauna of Lake Kultsjön, northern Sweden. *Rep. Inst. Freshw. Res. Drottningholm 46: 5—21.*

— and N.-A. NILSSON. 1965. On the food chain in some north Swedish river reservoirs. *Rep. Inst. Freshw. Res. Drottningholm 46: 31—48.*

GULLAND, J. A. 1962. The application of mathematical models to fish populations. *Brit. Ecol. Soc. Symposium II, editors Le Cren and Holdgate; 204—217.*

HOLT, S. J. 1960. Multilingual vocabulary and notation for fishery dynamics. *FAO, Rome: 1—42.*

LINDROTH, A. 1957. A study of the whitefish (*Coregonus*) of the Sundsvall Bay District. *Rep. Inst. Freshw. Res. Drottningholm 38: 70—108.*

LINDSTRÖM, T. 1954. Non-reproductive migrations in the char, *Salmo alpinus. Rep. Inst. Freshw. Res. Drottningholm 35: 118—132.*

— 1955. On the relation fish size—food size. *Rep. Inst. Freshw. Res. Drottningholm 36: 133—147.*

— 1962. Life history of whitefish young (*Coregonus*) in two lake reservoirs. *Rep. Inst. Freshw. Res. Drottningholm 44: 113—144.*

— 1964. Sikbeståndet i Barsele. *Inf. Sötvattenslab. Drottningholm 11.* Mimeographed. In Swedish.

— and N.-A. NILSSON. 1962. On the competition between whitefish species. *Brit. Ecol. Soc. Symposium II, editors Le Cren and Holdgate: 326—340.*

— and N.-A. NILSSON. 1964. Fiskbeståndet i Kultsjön. *Inf. Sötvattenslab. Drottningholm 8.* Mimeographed. In Swedish.

LÖTMARKER, T. 1964. Studies on planktonic crustacea in thirteen lakes in Northern Sweden. *Rep. Inst. Freshw. Res. Drottningholm 45: 113—195.*

NILSSON, N.-A. 1961. The effect of water-level fluctuations on the feeding habits of trout and char in the Lakes Blåsjön and Jormsjön, North Sweden. *Rep. Inst. Freshw. Res. Drottningholm 42: 238—261.*

— 1964. Effects of impoundment on the feeding habits of brown trout and char in Lake Ransaren (Swedish Lappland). *Proc. Intern. Ass. Limnol. XV: 444—452.*

NORDENG, H. 1961. On the biology of char (*Salmo alpinus*) in Salangen, North Norway. *Nytt Magasin for Zoologi, Oslo 10: 67—123.*

RICKER, W. E. and R. E. FOERSTER. 1948. The computation of fish production. *Bull. Bingham Oceanogr. Coll. 11: 173—211.*

RICKER, W. E. 1954. Stock and recruitment. *J. Fish. Res. Bd. Canada 11: 559—623.*

— 1958. Handbook of computations for biological statistics of fish populations. *Bull. Fish. Res. Bd. Canada 119: 1—300.*

RODHE, W. 1964. Effects of impoundment on water chemistry and plankton in Lake Ransaren (Swedish Lappland). *Proc. Intern. Ass. Limnol. XV: 437—443.*

RUNNSTRÖM, S. 1951. The population of char, *Salmo alpinus,* in a regulated lake. *Rep. Inst. Freshw. Res. Drottningholm 32: 66—78.*

— 1963. Rödingens lekvanor och vandringar i Borgasjön före och efter sjöns reglering. Mimeographed. In Swedish.

— 1964 a. Effects of impoundment on the growth of *Salmo trutta* and *Salvelinus alpinus* in Lake Ransaren (Swedish Lappland). *Proc. Intern. Ass. Limnol. XV: 453—461.*

— 1964 b. Kontroll av Jormsjöns lekrödingbestånd i Blåsjöälven. *Inf. Sötvattenslab. Drottningholm 4.* Mimeographed. In Swedish.

RUSSEL, E. S. 1931. Some theoretical considerations on the "overfishing" problem. *J. Conseil. Expl. Mer VI: 3—20.*

SIMPSON, A. C. 1956. The pelagic phase. In *Sea Fisheries, editor M. Graham, London: 207—250.*

SVÄRDSON, G. 1949—1957. The Coregonid problem I—VI. *Rep. Inst. Freshw. Res. 29, 31, 32, 33, 34, 38.*

— 1957. Skeppträsklöjan. *Svensk Fiskeritidskrift 66: 37—42.* In Swedish.

— 1962. Fiskevårdens teori. *Svenskt Fiske 5: 161—178.* In Swedish.

STUBE, MAJ. 1958. The fauna of a regulated lake. *Rep. Inst. Freshw. Res. Drottningholm 39: 162—224.*

TAYLOR, C. C. 1958. Convenor's report. The problem of sampling oceanic stocks which are partly demersal, partly pelagic, whose distribution differs with size and age, and which are fished by diverse techniques and by diverse countries. *ICNAF. Special publ. 1: 13—14.*

Limnological studies in Hyttödammen

2. Phytoplankton and its production

By ROLF ARNEMO and ARNOLD NAUWERCK

Institute of Limnology, Uppsala, Sweden

Contents

I. Introduction

In the first article of the series »Limnological studies in Hyttödammen» (ARNEMO 1964), information was given about the pond and its physical and chemical conditions. A review of earlier investigations concerning the pond was also included.

This second article presents the qualitative and quantitative composition of the phytoplankton and its production in Hyttödammen, with special regard to environmental factors.

The aim of the series of articles on Hyttödammen is primarily to contribute to a broader knowledge of Swedish ponds used for rearing fish. Investigations concerning phytoplankton in Swedish ponds were performed at Aneboda some forty years ago (NAUMANN 1925). Since that time, however, new

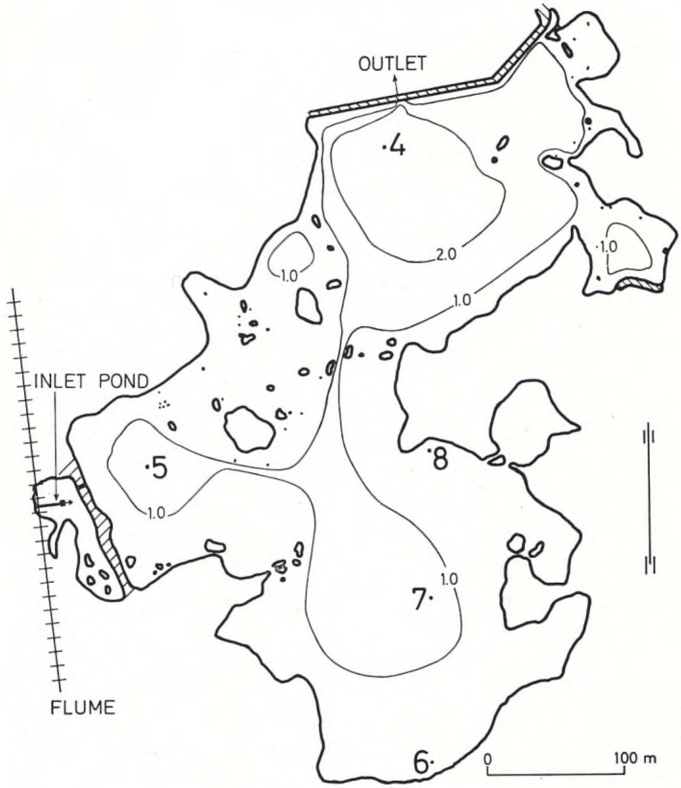


Fig. 1. Hyttödammen. The different sites and the depth contours.

methods have been introduced into limnology, especially the C^{14} technique for estimating primary production first described by STEEMANN NIELSEN (1952) and applied to lakes by RODHE (1958 a, 1958 b, 1962, RODHE *et al.* 1958). Since little is known of the primary production in ponds of the temperate zone, a secondary function of this article will thus be to contribute to knowledge about this type of water.

For the field work and primary production data Arnemo is responsible, while the analysis of the phytoplankton was contributed by Nauwerck.

II. Methods

1. Sampling sites

The sampling sites (Fig. 1) used in the present investigation are the same as sites 4, 5, 6, 7 and 8 used by ARNEMO (1964). The choice of the sites was explained in the same article, p. 12.

2. Phytoplankton

Samples for determining the qualitative and quantitative composition of the phytoplankton were collected with a plexiglass tube that takes an integrated sample from surface to bottom. After mixing the water column the samples for phytoplankton analysis and C^{14} exposure were taken. Thus only one sample was taken at each site. In one case, however, a series of samples from different depths was taken as a control. The samples were fixed with LUGOL's solution with 10 % acetic acid added (NAUWERCK 1963, p. 15). The examination of the samples (only fixed material) was made according to UTERMÖHL (1958), using an inverted microscope.

The quantitative data as cells per litre was converted into total volume with the aid of the specific volume of the single species (see RODHE *et al.* 1958).

3. Primary production

The technique used was that of STEEMANN NIELSEN (1952) with slight modification. During the winter the exposure took place from before sunrise until sunset the same day. During the summer the bottles were exposed from after the sunset one day until sunset the next day.

A complete series included bottles exposed at 0.1, 0.3, 0.5 and 1.0 m at sites 5, 6, 7 and 8. At site 4 another bottle was exposed at 2.0 m (bottom). Dark bottles were always incubated at 0.1 and 2.0 m at site 4.

On January 26, 1962, one bottle was exposed close to site 4 at an extra site where air bubbling through a perforated tube lying on the bottom prevented ice formation (see ARNEMO 1964, p. 10). Thus the light conditions differed from those at site 4, which was covered with 0.45 m ice. (A comparison of the results from the bottles exposed at the same depth of the sites, 0.5 m, showed a higher value of primary production at the ice-free site with 0.9 mg $C/m^3/day$ with 0.4 at site 4.)

On July 28—29, 1962, two series of bottles were exposed at site 6. The bottles in one series were filled with a mixed sample as described above. The bottles in the other series were filled with water from the same depth as where they were exposed. The samples were taken with a plexiglass tube with subsampling tubes at intervals as shown in ARNEMO (1964, Fig. 4 and pp. 13—14).

4. Light

Light measurements were performed according to ÅBERG and RODHE (1942, pp. 9 ff.). The filters used were BG 12, RG 2, and VG 9. Measurements were not undertaken at all the times when primary production was determined. On occasions when light measurements could not be made on the same day as primary production measurements, an attempt was made to measure light on a day with weather conditions similar to those prevailing on the day of exposure. Light penetration was always determined at site 4.

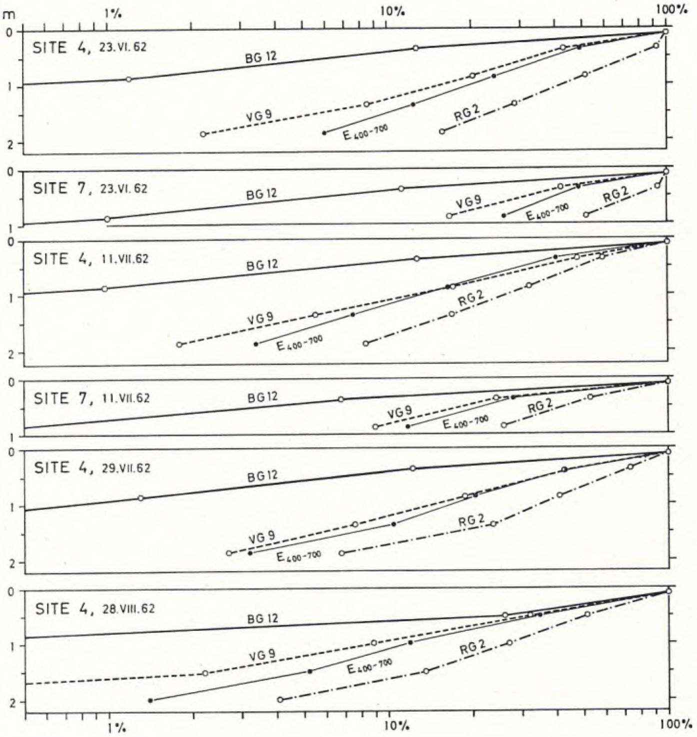


Fig. 2. Measurements of light penetration with different filters together with the calculated curve for visible light ($E_{400-700}$). Red=RG, blue=BG, green=VG.

At site 7 measurements were made as long as no vegetation had grown up. Helophyte and floating vegetation made it impossible to obtain proper measurements of light penetration at all sites except 4 and 6. The results obtained are given in Fig. 2.

Secchi disc transparency was measured at the deepest part of the pond. The transparency was often greater than the maximal depth. However, the values, given by ARNEMO (1964, Fig. 8) may help to give a more complete picture of the light climate in the pond.

III. Limitations

The collected material consists of a large number of samples representing considerable spatial and temporal variations. We have analysed the data in detail for possible patterns and interrelationships and in many cases our findings are not much more than indications. We hope at least to have clarified the problems involved in carrying out a field investigation of this kind.

A few of the most important limitations are summarized below. The remainder are included in the results section.

The possible effect of zooplankton upon the phytoplankton has not been regarded.

It is important to consider the reliability of the obtained values. A statistical treatment is lacking, but according to NAUWERCK (1963) the method used for obtaining phytoplankton volumes gives ± 10 % deviation. Therefore a difference of more than 20 % between samples is considered significant.

As NAUWERCK (1963, p. 20) and STANGE-BURSCHE (1963) have shown, patchiness in the distribution of phytoplankton exists even in a well-mixed, wind-exposed lake. In Hyttödammen, where horizontal mixing is sometimes lacking, and where occasional short-term locally bound irregularities in the distribution of phytoplankton may often occur, pronounced deviations between samples are to be expected. Such deviations therefore, may give no real information about the different sites in the pond.

As a rule, strong stratification is common in small ponds sheltered from the wind. However, the environmental factors of importance for the distribution of plankton in ponds change so rapidly that only samples taken at short intervals in time and space can give the information necessary for analysing the rapid changes in vertical distribution which are known to occur (WEIMANN 1942). A study of vertical distribution was not within the aims of the present investigation, and so only mixed samples from the water column were taken (see above, p. 143).

For the measurements using the C^{14} technique the reliability is perhaps somewhat better; however, statistical investigations about the horizontal deviation in short distances are lacking in the literature and so the authors have had to treat their values as if they were true.

It is possible that exposing the mixed samples at different depths inhibited or favoured certain species of algae adopted to a limited light regime in the water column (cf. WRIGHT 1964).

IV. Results

1. Composition of phytoplankton

The list of observed species (Table 1) is based only upon the quantitative samples; thus only species which on at least one occasion had a frequency of more than 10 cells per litre are taken in consideration. The list itself contributes valuable information about the biological characteristics of the pond.

The *Cyanophyta* were not especially numerous. Apart from *Anabaena Scheremetievii,* the species observed were ubiquitous. Of greater interest was the absence of certain forms: *Aphanizomenen flos-aquae* was not observed, nor was *Merismopedia* or other indicators of more pronounced eutrophy.

The *Chlorophyta* also gave the impression that the pond is rather poor in nutrients or in any case is not polluted. The composition was dominated by species that prefer clear water, e.g. *Gloeococcus Schroeteri, Pediastrum Boryanum, Dictyosphaerium Ehrenbergianum* while forms often found in more eutrophic or polluted waters such as *Scenedesmus quadricauda,* were entirely lacking. Colourless, heterotrophic species of the *Chlorophyta* were rather rare.

The *Euglenophyta* were also seldom seen. It is noteworthy that the species of *Trachelomonas,* common pond forms, were not observed in the samples.

The *Chrysophyta,* known to be generally sensitive to eutrophic waters, were next in importance to the *Chlorophyta.* At the same time, this group indicates more or less acid water. However, Hyttödammen is only slightly acid, as is witnessed by the small number of desmids and the comparatively large number of diatoms.

Among the *Diatomeae* the most typical representatives of eutrophy, such as *Melosira granulata, M. varians* etc. were lacking; but on the other hand typical indicators of oligotrophy, such as small *Cyclotella* species or *Melosira distans v. alpigena* were also lacking.

The picture was the same among the *Pyrrophyta.* As to the *Cryptomonadinae,* the "eutrophic" *Cryptomonas ovata* and *Chroomonas Nordstedtii* were not present. Among the *Dinophycinae,* the larger *Peridinium* species, such as the typical "eutrophic" form *Peridinium Voltzii,* were lacking.

The fungus *Cerasterias raphidioides,* present on a number of occasions, is not considered to be a special indicator of eutrophy. Other fungi and larger planktic bacteria which could possibly indicate eutrophy were also lacking.

2. Temporal and horizontal distribution of phytoplankton

Information about the quantities and the composition of the phytoplankton during the year at the different sites is given in Fig. 3 and Tables 2 and 3.

The *Cyanophyta* were apparently without quantitative significance. At the beginning of the summer *Anabaena flos-aquae* was found in small quantities, especially at site 5, but it disappeared during the course of the summer. The typical pond form *Anabaena Scheremetievii* (cf. RYLOV 1925) appeared during the summer in small quantities. Later in the summer *Oscillatoria splendida* appeared and was found in its highest concentrations near the bottom (see p. 150), occasionally together with *O. limosa.* In autumn both species diminished. During the period of investigation no indication of the typical fall maximum of *Cyanophyta* was found.

As is typical for most fresh waters, the *Chlorophyta* were the most important group as to number of species. Less typically, perhaps, in Hyttödammen, were also they the dominant group as to biomass. Seasonal changes in quantities and composition were only weakly pronounced. Most of the *Euchlorophycinae* were found at site 5 (*Tetraëdron, Scenedesmus, Selenastrum, Ankistrodesmus*). This site is apparently influenced by the transport of phytoplankton from the Dalälv river to the pond through the flume, which takes water from the river at a place where the stream is only very weak. (For details about the composition of the phytoplankton of the Dalälv river

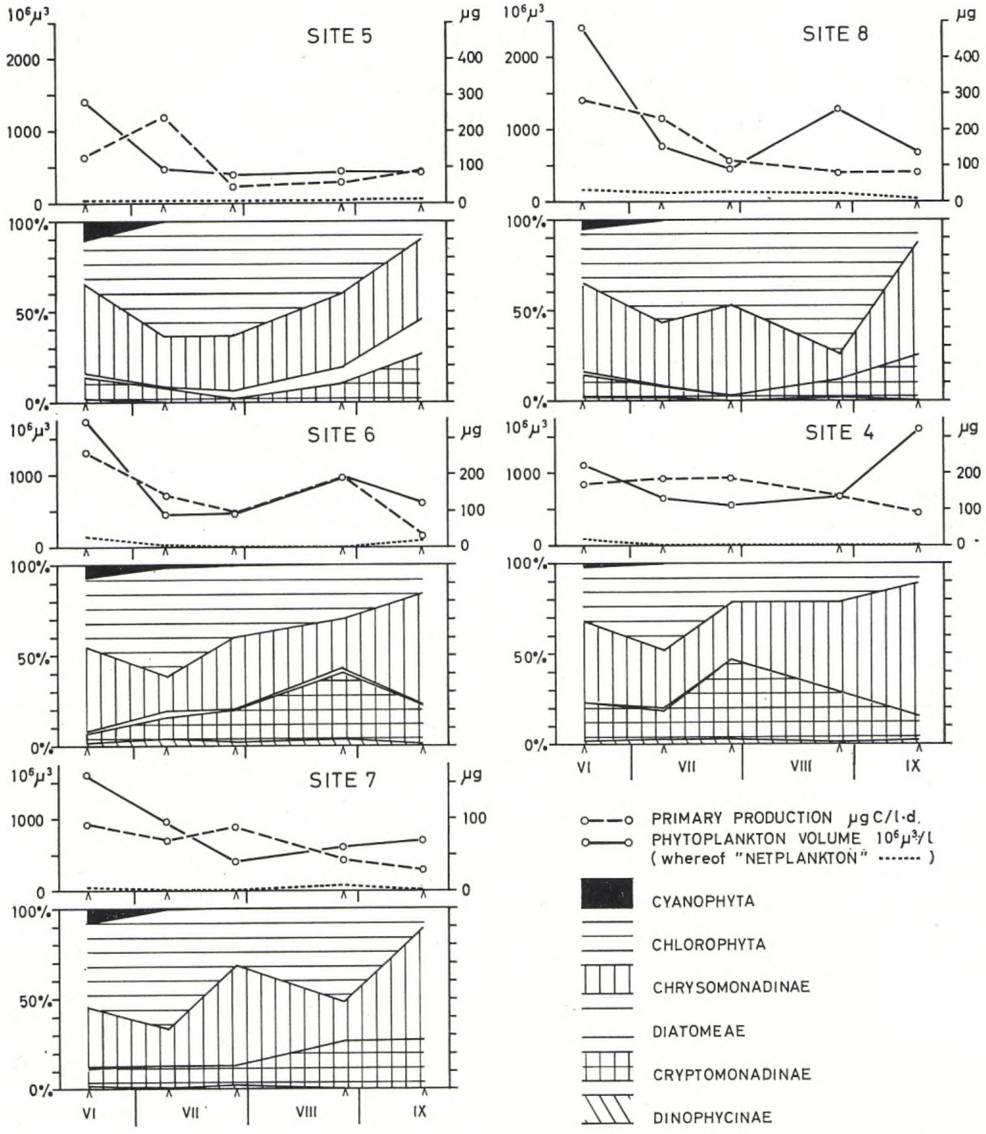


Fig. 3. Primary production, total phytoplankton volume and phytoplankton composition by percentage of total volume at the sites.

see SKUJA 1956). At the beginning of the investigation the phytoplankton everywhere in the pond was dominated by *Ankistrodesmus* together with *Chlorella*- and *Coccomyxa*-species. During the same period the *Volvocales*, e.g. *Volvox*, as a rule common in ponds, were observed only in low numbers. The *Chlorophyta* had a minimum on July 28. Following that, small *Chlamydomonas* (cf. *gloeopara* SKUJA) and small swarm spores dominated everywhere except at site 5. As the end of the investigation period approached the species composition remained about the same but the quantities diminished.

Botryococcus Braunii was found regularly, but only in low numbers. The *Conjugatae* were few in number, being represented only by some *Closterium* species (*C. Kuetzingianum, C. acicularis v. subpronum* and others).

The *Chrysomonadinae* were abundantly represented at the beginning of the period of investigation by *Uroglena americana* and *Chromulina.* At this time *Erkenia subaequiciliata* was found only at sites 5—8. *Dinobryon acuminatum* and *Mallomonas akrokomos* were moderately common. Later on, numerous small *Chrysomonadinae* such as *Erkenia* were always present. They diminished somewhat, but from August they again became more abundant as species and individuals. On July 28, however, *Erkenia* was only found at site 4 and later on only at site 5. Non-pigmented chrysomonads were especially numerous on July 28. On August 27, *Mallomonas akrokomos* was again comparatively abundant in number. On September 18, other species of *Mallomonas, Dinobryon* and *Pseudokephyrion* were found, although in smaller quantities.

The *Euglenophyta* were without significance both qualitatively and quantitatively.

The *Diatomeae* were of little quantitative significance. Perhaps the absence of a spring outburst of diatoms, e.g. small *Stephanodiscus* species, was due to the late filling of the pond with water in the spring. Several species were found primarily at site 5, such as *Tabellaria, Diatoma, Melosira islandica ssp. helvetica,* the latter especially in June and in September. In June at site 5 there was a comparatively large number of individuals of *Rhizosolenia eriensis* (cf. SKUJA 1956, also in the plankton of the Dalälv). *Cyclotella* (*comta*), *Synedra acus* and *S. ulna* (*v. danica*) occurred sporadically at all the sites except site 4. In July and August the *Diatomeae* were almost completely lacking.

The *Cryptomonadinae* were the group that showed the most evident differences in time and space. In addition, they were very important quantitatively even though they were represented by only a few species. *Katablepharis ovalis* was always found in large numbers in the whole pond during the entire period of investigation. Further, *Rhodomonas minuta, R. lacustris* and *Cryptomonas Marssonii* were numerous especially at the beginning and the end of the period of investigation. *Cryptomonas erosa* was comparatively less numerous. *Rhodomonas minuta* consistently had its highest frequency at site 4 and its next highest at site 6, the only exception being in August when the highest values were at site 6 and the next highest at site 5. In June there was a pronounced maximum of *Cryptomonas erosa* at site 7. In July the *Cryptomonadinae* were at a minimum, and on July 28 they were in extremely low numbers at site 5 and site 8.

The *Dinophycinae,* as a rule common in ponds, were represented in Hyttö-

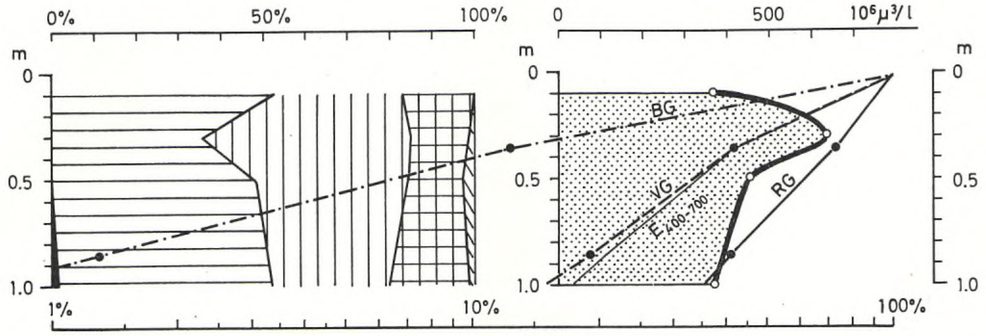


Fig. 4. Vertical distribution of phytoplankton at site 6 on July 28; on the left as composition by percentage of total volume and on the right as total volume. Penetration of red (RG), blue (BG), green (VG) and of the calculated visible light ($E_{400-700}$) at site 4 on July 29 as percentage of the light measured immediately under the surface. Lowest scale (logarithmical) is for the light.

dammen only by nannoplanktic species of *Gymnodinium* and *Amphidinium*. At the beginning of the investigation period these forms were present in large numbers, but they diminished as time went on. At site 5 they were always least in numbers and in the beginning of July, they were completely lacking. In the autumn they were found only at site 4. It is also noteworthy that *Amphidinium Lohammari* (cf. SKUJA 1956) was found at the beginning of July.

The planktic fungus *Cerasterias raphidioides* was only observed in small numbers.

As to the quantitative values, it can be said that they were neither very large nor very small. As a rule they lay between 10^4 and 10^5 cells per litre for the frequent species. The "small monads" were in the order of 10^6 cells per litre and only the µ-algae occasionally reached concentrations as high as 10^8 cells per litre. The numbers were never those found during a water bloom. In such cases the cell count per litre is generally at least about 10^1—10^2 times higher; in ponds the small *Protococcales* can occur 10^3 or 10^4 times as high as those found here.

In summary, the list of species (Table 1) and the condensed list of quantitative data (Table 2) show the following:

1. The number of forms with significant quantitative representation is comparatively large.
2. Pronounced mass outbreaks of one or several species did not occur.
3. Only a few species were regularly observed at all the sites in the pond, while irregularities in the horizontal and temporal distribution were the rule. In absolute values, however, these irregularities are still moderate.
4. Certain differences existed between the sites as to the quantities and the

composition of plankton. At site 5 the plankton transport to the pond from the Dalälv was regularly noticeable. This was especially true for the *Diatomeae,* which were found almost exclusively at site 5. The *Cryptomonadinae* were always highest in number at sites 4 and 6. On August 27, a large maximum of small swarm spores and small *Chlamydomonas* was observed at site 8. A diminishing gradient was evident, with lesser numbers at sites 6 and 7 and practically none at sites 4 and 5.

3. Vertical distribution of phytoplankton

To get at least some information about the vertical distribution and at the same time to compare the mixed samples with a real vertical distribution, on July 28 both a mixed sample and a series of samples from different depths were taken. The results are given in Fig. 4 and Tables 2 and 3 (in Fig. 4 and Table 3 a and b as volumes, cf. p. 143).

If the mean values for the total quantity of the two series from July 28 in Table 3 a and b are compared it can be seen that they differ by less than 5 %. Quantitative percentage composition among the compared groups shows a great degree of difference, and the largest difference occurs in some single species, e.g. *Rhodomonas, Ankistrodesmus* and, above all, *Oscillatoria.*

The differences when comparing the groups were without any doubt within the statistical limits for the methods used. In fact, the differences between the mean values of the quantities were so small that the agreement must be said to be remarkably good. On the other hand, the differences as to *Oscillatoria splendida* cannot be explained by means of random scattering. The most probable explanation of the differences is that it is an expression of an irregular horizontal distribution of plankton even with respect to very small distances. However, it is practically impossible to take a sequence of samples in exactly the same place from a boat. It is also very difficult to avoid any influence from the boat upon the plankton distribution. But it is obvious from the series of samples showing the vertical distribution that taking mixed samples of the water column, as in the present investigation, was the best method, especially in view of the purposes and the limitations pointed out above (see p. 144—145).

The vertical distribution showed a less pronounced stratification than was expected. All the observed species were lowest in number near the surface, which might be explained by the inhibiting effect of too much light. Most of the species showed a maximum at 0.3 m.

WEIMANN (1933, Fig. 10) suggested a vertical distribution of the different groups of algae for ponds similar to that of RUTTNER (1929) for a deep lake; this distribution was not fully realized here. The *Chlorophyta* and *Chrysomonadinae* showed the highest value at 0.3 m. The *Dinophycinae* showed a maximum lying somewhat deeper, and *Oscillatoria* and *Cryptomonas* showed their highest values near the bottom. Thus some of the species followed the expected picture. (*Oscillatoria splendida* is not a typical planktic form and its vertical distribution is not necessarily caused by light.) However, *Rhodomonas minuta* and *R. lacustris,* so far as could be observed, had their maxima near the surface or were homogenously distributed vertically. This agrees with the observations made by WRIGHT (1964) in a shallow lake. In deeper lakes, however, these species almost always are found at depths where the light intensities are low (RUTTNER 1929, NAUWERCK 1963). Certainly the temperature conditions can help to explain the weakly pronounced vertical distribution. But this does not explain the regularly more abundant occurrence of the *Cryptomonadinae* at site 4, where the depth is greater and for that reason the light conditions are better for this group.

Even if the vertical distribution in Hyttödammen was only weakly pronounced, there is general agreement between WEIMANN's observations and the results obtained. It must also be taken into consideration that some groups known to have their maximum immediately above the bottom sediments were somewhat underrepresented in the mixed samples. When using the plexiglass tube, the last centimetres of the water column above the bottom sediments must be left behind if an undesirable mixing of material from the sediments is to be avoided.

4. Primary production

In Fig. 5 a and b are given data showing the primary production. The numbers indicating the primary production in the layers 0—1 m and 1—2 m are given to the right of the corresponding curve. The dark assimilation, the values of which are given in Table 4, has been subtracted. When the pond was ice-covered the number indicates the primary production in a reduced layer from the under limit of the ice to 1 m. On March 13 and April 10, the primary production was measured only at 1.0 m, except at site 4. The numbers at the curves from these occasions thus indicate the primary production only at that depth and not the whole layer.

From Fig. 5 it can be seen that the values from the winter were very low at all the sites. No significant spatial difference could be observed. If the site that had the highest value in the layer 0—1 m is listed from time to time, starting with the results from June 17—18, no regularities or tendencies can be noted.

The sites with the highest values observed for a given date are as follows: on June 17—18 sites 6 and 8, on July 9—10 site 5, on July 28—29 sites 4 and 7, on August 27—28 site 6, on September 18—19 sites 4, 5 and 8, on October 24—25 site 5. In the same order of time the sites where the lowest values were observed were: site 5, site 8, site 5, site 5, site 6, sites 6, 7 and 8. Thus site 5 was always among either the highest or the lowest values.

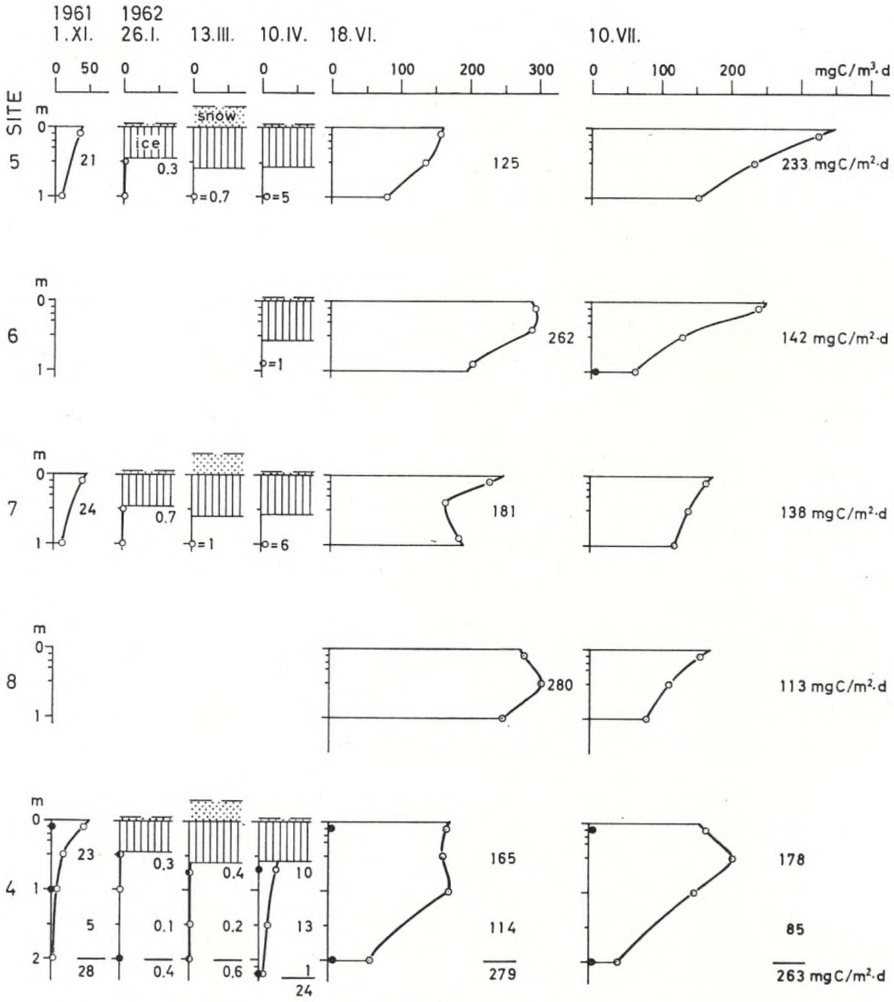


Fig. 5 a. Temporal and spatial distribution of the primary production.

On July 28—29 at site 6, two kinds of series were exposed (cf. p. 143 and p. 150). The results show some interesting differences. The values of total assimilation were 96 mg C/m^2/d for the series where samples from the mixed water column were exposed, and 72 mg C/m^2/d for the samples exposed at the same depths as they were taken. The curves also differed in shape. The former showed an apparent light-inhibiting effect near the surface and a maximum at 0.3 m. The latter showed no light-inhibiting effect and no maximum at 0.3 m. The difference in the total assimilation was due to the different shape of the curves in the first 0.5 m.

In ponds, which as a rule are shallow, the curve of primary production generally consists of an optimum layer and little decrease with depth (cf. Fig.

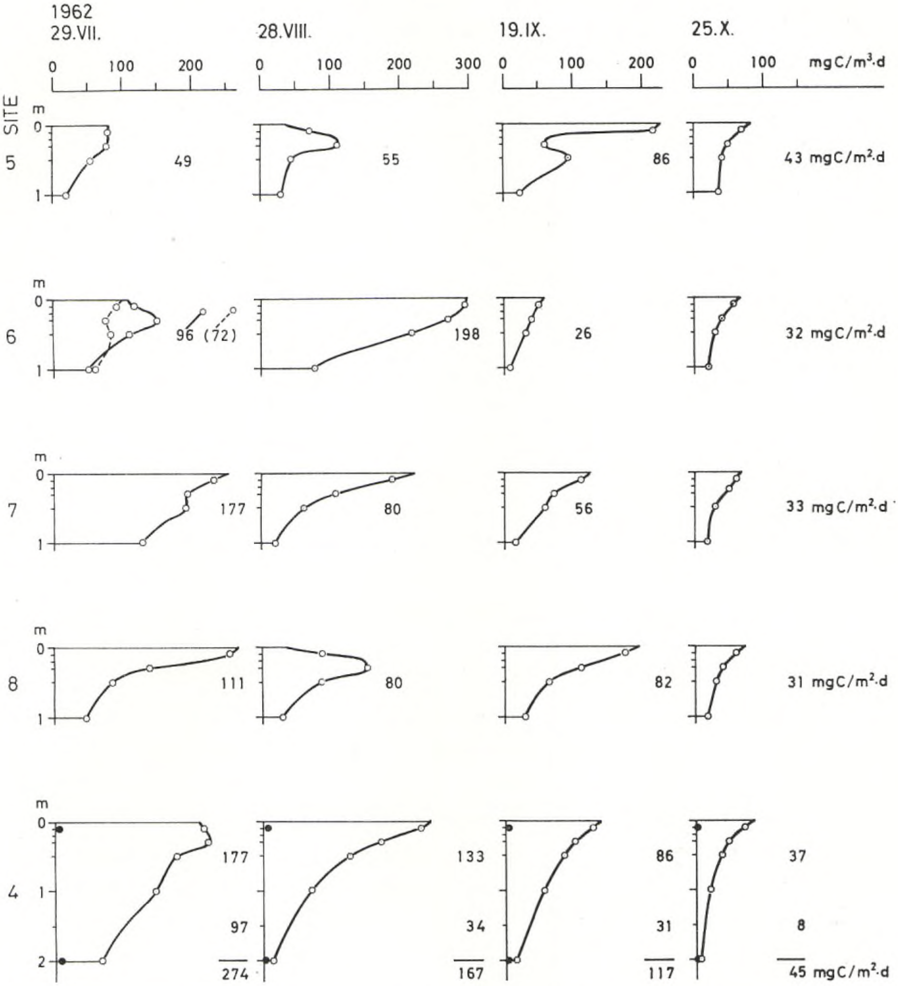


Fig. 5 b. Temporal and spatial distribution of the primary production.

5, sites 5—8 on June 17—18). But the presence of higher aquatic vegetation is one of the factors that might influence the light climate and thus primary production. In Hyttödammen, with its uneven distribution of higher aquatic vegetation, chiefly *Sagittaria sagittifolia* L. (see ARNEMO and NORLIN 1962 for map of vegetation), the light below the surface might differ very much from area to area. Thus on days of bright sunshine (see July 28—29) one might expect a continuum from optimum production throughout the water column at sites free of vegetation to a more or less reduced optimum production layer closest to the surface at sites with dense vegetation (sites 5, 7 and 8). As is shown in Fig. 5, this was not found, however, owing to the methods used. As discussed above (p. 153), species which probably prefer a limited light regime at a given depth are exposed at different depths. The primary production curves indicate that such light adaptation is of great importance.

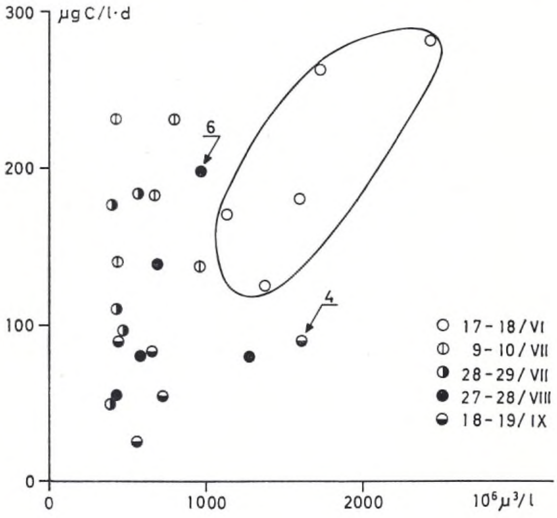


Fig. 6. Ratio of primary production to total phytoplankton volume. Mean values from the sites at different times. See text for further explanation.

V. Discussion

1. Phytoplankton volume and primary production

In order to get an expression of the efficiency of CO_2 assimilation, total phytoplankton volume (Fig. 3) was plotted against assimilation (Fig. 5) for each occasion of measurement in Fig. 6.

Fig. 6 shows that there is no evident correlation between phytoplankton volume and assimilation. This seems surprising in view of the results obtained by RODHE *et al.* (1958) and NAUWERCK (1963) showing a rather good correlation with similar data from Lake Erken. The probable causes of the divergent results obtained in Hyttödammen are several.

First, the samples are taken at long intervals in time, and the number of data may be too small. It is possible that more frequent sampling might have given another picture. Second, strictly speaking, only data from one site may be compared over time, although one may also compare the volumes from all the sites on a given occasion. Making these two comparisons, the present material shows no correlation in the former case and in the latter case a correlation exists only on the first and — weakly — the fourth occasion of sampling (see Fig. 6). The material obtained on the fourth sampling was characterized by irregularly distributed small swarm spores and *Chlamydomonas* (cf. p. 147). If these algae are not taken into consideration the weak correlation disappears on this occasion too. On all the other dates of sampling we can find strongly differing assimilation values for more or less the same values of volume.

A possible explanation could be the different composition of the plankton in time and space. Some extreme values might thus be explained, namely point 4 in Fig. 6, where non-pigmented monads are rich, and point 6 in Fig. 6, where *Cryptomonadinae* are dominant. In the first case the assimilation per volume is especially low, in the second case especially high.

Another reason for the lack of a clear relationship between algal volume and assimilation might be differences in age and physiological condition of the algae. The observations of RODHE *et al.* (1958) and NAUWERCK (1963), however, do not support this theory: their material, collected over a whole year, was comprised of algae of quite different taxonomic groups as well as algae of different physiological conditions. Furthermore, in the present study a clear correlation existed between volume and assimilation on only one occasion. It is hard to believe that in four—fifths of all cases the physiological condition of a mixed association of algae would overshadow the importance of the volume of algae.

Finally, different environmental factors at different places and time must be regarded as a possible explanation. At the time of the first sampling the pond had no higher aquatic vegetation. The efficiency of assimilation under these conditions may depend mainly on the volume. Later on it might be inhibited or improved through shading by the vegetation. Another possibility is stimulation or inhibition by metabolic products from the higher aquatic vegetation. In this respect, however, site 4, which was always free of higher vegetation, is comparable to the situation represented by the first sampling, when the entire pond was free of higher aquatic vegetation. But even if the assimilation is plotted against volume only at site 4 no correlation can be observed. Consequently, the possible effect of metabolic products cannot be clearly established.

2. Effects of environmental factors upon phytoplankton and primary production

Even though it is well known that there are always several factors at work simultaneously in ecological situations, the environmental factors will be treated individually in what follows. This will be done in order to examine the relative importance of the individual factors. Indeed, the nature of the present material does not permit an examination of the combined effect of, e.g., light and temperature. When comparing phytoplankton and production on one hand and environmental conditions on the other it must be remembered that the phytoplankton is the result of earlier prevailing environmental conditions but their assimilation is dependent on both the instantaneous conditions and the previous conditions. Temperature and light certainly have a direct influence upon assimilation. The temperature also characterizes to a certain extent the earlier prevailing conditions. On the other hand the nutrient concentrations at times of sampling probably give little information about previous conditions.

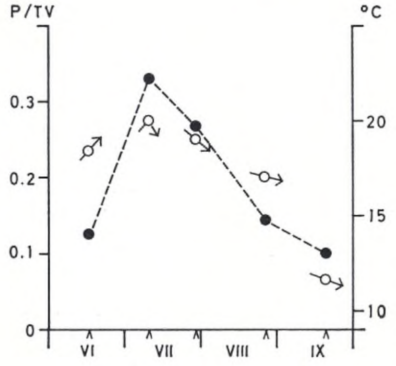


Fig. 7. Assimilation efficiency $\left(\frac{P}{TV} = \frac{\text{Primary production as mg C/m}^2 \cdot \text{d}}{\text{Total phytoplankton volume as mm}^3/\text{m}^3} \right)$ and temperature. The arrows indicate the actual tendency of the development of temperature for each sampling occasion. Mean values from the whole pond.

(a) *Light.*

As the measurements of light are restricted to determination of the gradient of light (Fig. 2), most of the comments that can be made are given above in connection with the vertical distribution of phytoplankton (p. 150). The curves for the primary production do not give any information concerning the relationship between light and production. Irregularities in the curves (site 6, July 29) could possibly be explained by the fact that some species were exposed at depths where they did not naturally occur and thus may have been stimulated or inhibited (cf. p. 145). However, data confirming this possibility are lacking.

(b) *Temperature.*

The measurements of temperature showed (ARNEMO 1964) that the horizontal spatial variations in temperature were without significance. The same may be said for the vertical spatial temperature variations (on July 28 only 2° difference between surface and bottom). Furthermore, any thermal stratification that exists is brief, because of the almost continual circulation.

Within certain limits a higher assimilation efficiency can be expected at higher temperatures. Fig. 7 shows that the mean efficiency of assimilation at all the sites is fairly well correlated with the mean temperature of the pond. As was shown in the discussion of temporal and horizontal distribution of the phytoplankton (pp. 146) the succession of the dominating groups was *Chrysomonadinae-Chlorophyta-Cryptomonadinae-Chrysomonadinae.* The efficiency of assimilation was low at the beginning and lowest at the end of the period of investigation. However, the temperature differed very much on the two occasions and has to be kept in mind. The highest values of assimilation efficiency lie in the middle of the times of highest temperature. It would seem as if these values were caused by the *Chlorophyta*, which were dominant. However, the species composition at the different times must be taken into consideration. In June there may have been a senescent population of spring forms. In the summer were found *Mallomonas, Dinobryon* and others, which apparently respond quite differently to higher temperature.

The *Cryptomonadinae,* which dominated the phytoplankton at the end of the investigation period, showed the lowest efficiency of assimilation. However, taking into account the low temperature, their efficiency is to be considered high, indicating that this group is well adapted to autumn conditions.

3. Characteristics of the sites

It is of importance for an understanding of the production biology of the pond to examine whether there is a significant difference persisting through the summer between the sites or whether the observed differences are only occasional. As has been said concerning the limitations of this investigation, a broad statistical scattering is to be expected. The comparison of the mixed sample with the actual vertical distribution on July 28 confirms that the differences in space as to the quantitative distribution are not significant. Furthermore, there is no reason to assume that the observed differences in quantities between the different sites on any given occasion of sampling must be explained by the different character of the sites. As is clear from p. 154—5 above, the quantitative differences are hardly to be considered as significant.

In contrast to the quantitative data, the qualitative data are able to give information about the significance of the differences in time and space. On pp. 146—150 this aspect has already been discussed in regard to the phytoplankton. If we summarize the statements about phytoplankton and the other results of this and earlier investigations (ARNEMO 1964), we get the following picture.

As ARNEMO (1964 pp. 15—18) has shown, site 5 is influenced throughout the summer from water from the Dalälv and the vegetation, with contribution from some springs, causes a horizontal heterogeneity to be built up successively in the south-eastern bay. The result is that site 5 obviously is characterized by the incoming water from the Dalälv. The proportion of phytoplankton that is not endemic to the pond is quite remarkable, and the environmental conditions compare unfavourably with these of the rest of the pond; the content of nutrients, especially, is lesser in the Dalälv water than in the pond.

Sites 6, 7 and 8 are influenced by water characterized by, e.g., higher specific conductivity and a higher content of calcium, bicarbonate and nitrogen in a decreasing degree from site 6 to 8. As a rule it is during times when the bay has little or no exchange with the other parts of the pond that the highest production is found, with a centre at site 8 and a decreasing gradient at sites 7 and 6. This is reflected also in a gradient for the phytoplankton. From site 6 to 8 an increasing proportion of *Chlorophyta* (and occasional *Cyanophyta*) is found. In the reverse situation more *Cryptomonadinae,* here especially *Rhodomonas minuta* and *R. lacustris*, are to be found.

It is noteworthy that the *Cryptomonadinae* seem to have lower requirements for nutrients. The highest number, as mentioned above on p. 148, were found at site 4, again at a high proportion of nitrogen, but at lower absolute values of nutrient salts.

Furthermore site 4 is characterized by a thicker layer of optimal assimilation and by a less intense decrease of assimilation with depth. Although these observations are without doubt reliable, neither the composition and quantities of phytoplankton nor the environment factors (which are similar to those of site 5) give information about the possible causes of the observation.

It is interesting to find that at the beginning of the period of investigation the species composition of the phytoplankton was quite similar at the different sites. At first the development was more or less parallel, too. Later on the sites developed their own character, which began with increasing dominance of different species at different sites. After that, the development continues towards a maximum relative individuality of the sites at the end of the period. This relative individuality was as a matter of fact moderate and was expressed less by the dominating species than by the accompanying species, in this case especially by different *Chrysomonadinae*.

The question whether significant differences between the sites in time and space are to be found can thus be answered. The pond consists of three parts which differ significantly from each other. To be sure, their biological and environmental conditions are largely characterized by water from the Dalälv. However, no one site could characterize the pond as a whole. Furthermore, the results from sites 6, 7, and 8 in the south-eastern bay of the pond make it obvious that important horizontal heterogeneity exists within short distances, a result which supports the critical points of view of WEIMANN (1942) concerning investigations about the classification and dynamics of shallow waters.

4. Comparison with results of other authors

In recent years the classification of waters has changed from an earlier static way of looking at things to a dynamic one, based upon the productivity. Thus, RODHE (1958) suggested a classification system based upon the primary production.

To begin with, one can classify Hyttödammen by the following older systems and according to them it is: (1) After NAUMANN (1925), "lowest cultural type"; with respect to the plankton, "the higher natural type". 2. After NAUMANN (1927), autotrophic, oligotrophic. (3.) After WEIMANN (1942), apparent oligotrophic clear-water pond. (4) After LIEBMANN (1951) in his revision of the saprobysystem from KOLKWITZ and MARSSON, between β-mesosaprobic and oligosaprobic.

More concretly, the pond is characterized by moderate numbers of *Chrysomonadinae, Chlamydomonas* and *Cryptomonadinae,* and waterblooms never occur but it has a rather high primary production.

Earlier works concerning environmental factors and phytoplankton in ponds are frequent. Among the most important of these are DIEFFENBACH and SACHSE (1912), SCHAEDEL (1917), ATKINS and HARRIS (1924), RYLOV (1925), NAUMANN (1925, 1927), GESSNER (1934), NYGAARD (1938), VON MITIS (1941) and WEIMANN (1933, 1935, 1942). The results of these works are competently discussed and analysed by WEIMANN (1942). His results and conclusions are still valid (LIEBMANN 1960). The present article can support the thesis of WEIMANN as to phytoplankton and chemical conditions. Our results and difficulties also confirm his conception of the pond environment.

The main subject of the present article, however, is the relation between the primary production and phytoplankton and as such to contribute to a broader knowledge of ponds.

Many investigations have been performed using the C^{14} technique to determine the primary production of phytoplankton, since the method was described by STEEMANN NIELSEN. But they are almost entirely restricted to lakes and sea water. The only results from investigations of ponds in the literature seems to be by WETZEL (1964). But the environment investigated by him was very saline. Therefore the values found in Hyttödammen can only be compared with those from lakes. A comparison seems suitable between Hyttödammen and Lake Erken in Uppland, since, of the lakes for which results have been published, Lake Erken lies closest geographically to Hyttödammen (about 100 km to the south-east). Approximately the same climatic conditions can be assumed to prevail at Lake Erken and Hyttödammen. The comparison will be made in two ways: as production in the layers 0—1 and 1—2 m, and under a given surface area.

STEEMANN NIELSEN and AABYE JENSEN (1957) proposed that the depth where 1 % of the light in the water occurs will be the lower limit of the trophogenic layer. As is shown in Fig. 2, in Hyttödammen this depth lies at about 2.7 m on June 23 (extrapolated) and changes to 2.0 m on August 28. In Lake Erken it lies between about 9 and 11 m in the summer. Thus Hyttödammen's light climate differs very much from Lake Erken's. As shallow ponds mostly consist only of an optimum production layer, there is an essential difference when comparing them with a lake.

Neglecting the possible influence of higher vegetation, a comparison of primary production in Lake Erken and Hyttödammen for the layers 0—1 and 1—2 m gives the following results. The values for Lake Erken have been taken from the primary data in the material studied by RODHE *et al.* (1958).

	$mg\ C/m^3 \cdot d$						$mg\ C/m^2 \cdot d$			Time of sampling
	0—1 m			1—2 m						
	mean	range	n	mean	range	n	mean	range	n	
Hyttödammen	133	26—280	25	77	35—120	5	147	26—280	25	June—Sept. 1962
Lake Erken	117	28—404	35	109	29—390	35	430	140—1,272	35	June—Sept. 1954—55

n=number of samples.

The production in Hyttödammen is about 15 % higher in the layer 0—1 m and about 30 % lower in the layer 1—2 m when comparing the mean values of Lake Erken and Hyttödammen. Even though only few data are available this conclusion appears to be well-founded. (Compare the depths of the trophogenic layers.)

Among the lakes studied by RODHE (1958 a, Fig. 8 and 1958 b, Fig. 7) the primary production in mg C/m^3/d in Hyttödammen falls within the same range as most of the values of Lake Erken and Görväln. But the primary production per unit area at the same time was lower, as was shown in the Table. Thus, Hyttödammen can be ranked somewhere between oligotrophy and eutrophy *sensu* RODHE.

VI. Summary

Investigations of the qualitative and quantitative composition and the primary production of the phytoplankton were made in Hyttödammen, a 12 ha pond for the rearing of first-summer or one-year-old salmon. In the winter of 1961/62 samples were occasionally taken for studying the primary production. The pond was drained and refilled between late April and the beginning of June 1962. From that time on, samples were taken until October, at about monthly intervals, for studying the primary production and the phytoplankton. Mixed samples from the whole water column were taken with a plexiglass tube and the primary production was studied using the C^{14} technique. Phytoplankton analyses were performed using the Utermöhl technique.

The phytoplankton composition was numerically dominated by *Chlorophyta* (e.g. *Chlamydomonas, Ankistrodesmus, Coccomyxa*), *Chrysomondinae* (small monads as *Chromulina*) and *Cryptomonadinae* (*Rhodomonas, Cryptomonas*). By volume the *Chrysomonadinae* (max. *c.* 1,200 $\mu^3 \cdot 10^6$/l), the *Chlorophyta* (max. *c.* 1,000 $\mu^3 \cdot 10^6$/l and the *Cryptomonadinae* (max. *c.* 400 $\mu^3 \cdot 10^6$/l) dominated.

The horizontal distribution was influenced, in the vicinity of the inlet of the Dalälv water, by phytoplankton that had been transported via the flume from the Dalälv. Some differences were also observed when comparing other parts of the pond.

The mean values of total volume, studied at 5 sites, ranged between 457 and 1,648 $\mu^3 \cdot 10^6$/l. The highest values were obtained in samples taken in the middle of June and the lowest from samples taken in late July.

The mean values of primary production at 5 sites ranged between 73 and 225 mg C/m^2/d in the summer. The highest values were obtained in the middle of June and thereafter they successively diminished, the lowest values occurring in October.

The mean efficiency of assimilation (primary production in relation to total

volume of phytoplankton) was highest in July, lesser values being observed before and after that time.

The horizontal spatial differences as to primary production were large, but no significant variation could be observed.

Based upon the primary production of the phytoplankton (*sensu* RODHE) Hyttödammen is ranked somewhere between eutrophy and oligotrophy.

VII. Acknowledgments

We gratefully acknowledge the help accorded us by:

Professor W. RODHE, head of the Institute of Limnology, who read the manuscript critically and made many valuable suggestions;

Miss A. PANDERS, who made the radioactivity measurements and the drawings;

Dr. R. WRIGHT, who helped with the English version.

Financial assistance for the field work was given by the Royal Fishery Board of Sweden and the foundation "Främjande av ograduerade forskares vetenskapliga verksamhet" at the University of Uppsala.

VIII. References

ÅBERG, B., und RODHE, W., 1942. Über die Milieufaktoren in einigen südschwedischen Seen. *Symb. Bot. Ups. 5 (3).*

ARNEMO, R., 1964. Limnological studies in Hyttödammen. 1. Physical and chemical conditions. *Rept. Inst. Freshw. Res., Drottningholm 45, 5—93.*

— och NORLIN, Å., 1962. Om vegetation och miljö i Hyttödammen vid Älvkarleby. *Södra Sveriges Fiskeriför. 1959—60, 42—50.*

ATKINS, W. R. G. and HARRIS, G. T., 1924. Seasonal changes in the water and heleoplankton of fresh-water ponds. *Sci. Proc. Roy. Dublin Soc. N. S. 18.*

DIEFFENBACH, H. und SACHSE, R., 1912. Biologische Untersuchungen an Rädertieren in Teichgewässern. *Int. Rev. Hydrobiol., Biol. Suppl. 3.*

GESSNER, F., 1934. Nitrat und Phosphat im Dystrophen See. *Arch. Hydrobiol. 27. 131—161.*

KARLGREN, L., och NAUWERCK, A., 1958. Undersökning av Tämnarån 1957. Maskinskrivet manuskript, Limnologiska inst., Uppsala.

LIEBMANN, H., 1951. Handbuch der Frischwasser- und Abwasserbiologie. Bd 1. München.

— 1960. Handbuch der Frischwasser- und Abwasserbiologie. Bd 2. München.

VON MITIS, H., 1941. Ökologische Studien am Lusthauswasser, einem Altwasser im Prater von Wien. *Arch. Hydrobiol. 37, 426—465.*

NAUMANN, E., 1925. Undersökningar över fytoplankon i dammar vid Aneboda fiskeriförsöksstation åren 1911—1920. *Lunds Univ. Årsskr. N. F. Avd. 2 Bd. 21 nr. 1.*

— 1927. Die Definition des Teichbegriffs. *Arch. Hydrobiol. 18, 201—206.*

NAUWERCK, A., 1963. Die Beziehungen zwischen Zooplankton und Phytoplankton im See Erken. *Symb. Bot. Ups. 12 (5).*

NYGAARD, G., 1938. Hydrobiologische Studien über dänische Seen und Teiche. *Arch. Hydrobiol. 32, 523—692.*

RODHE, W., 1958 a. Primärproduktion und Seetypen. *Verh. internat. Ver. Limnol. 13, 121—141.*

— 1958 b. Aktuella problem inom limnologien. *Svensk naturvetenskap, 11, 55—107.*

— 1962. Sulla produzione di fitoplancton in laghi trasparenti di alta montagna. *Mem. Ist. Ital. Idrobiol., 15, 21—28.*

Rodhe, W., Vollenweider, R. A. and Nauwerck, A., 1958. The primary production and standing crop of phytoplankton. Perspectives in marine biology, Univ. California press. Berkeley and Los Angeles, 299—322.

Ruttner, F., 1929. Das Plankton des Lunzer Untersees, seine Verteilung in Raum und Zeit während der Jahre 1908—1913. — *Int. Rev. Hydrobiol. 23: 1—138.*

Rylov, W. M., 1925. Über das Neuston in einem Teiche der Umgebung von Alt-Peterhof (Gouv. Petersburg). *Arch. Hydrobiol. 15, 497—508.*

Schaedel, A., 1917. Produzenten und Konsumenten im Teichplankton, ihre Wechselwirkung und ihre Beziehung zu den physikalischen und chemischen Milieueinflüssen. *Arch. Hydrobiol. 11, 404—457, 511—564.*

Skuja, H., 1956. Taxonomische und biologische Studien über das Phytoplankton schwedischer Binnengewässer. *Nov. Acta Soc. Sci. Upsal. Ser. IV, 16, 3.*

Stange-Bursche, E.-M. 1963. Beobachtungen und Untersuchungen über die horizontale Planktonverteilung in Seen. *Arch. Hydrobiol. 59, 351—372.*

Steemann Nielsen, E., 1952. The use of radio-active carbon (C^{14}) for measuring organic production in the sea. *J. du Conseil 18, 117—140.*

— and Aabye Jensen, E., 1957. Primary oceanic production. The autotropic production of organic matters in the oceans. *Galathea rep. Scient. res. of the Danish deep-sea exp. round the world 1950—1952. I, 49—136.*

Utermöhl, H., 1958. Zur Vervollkomnung der quantitativen Phytoplanktonmethodik. *Mitt. internat. Verein. Limnol. No. 9.*

Weimann, R., 1933. Hydrobiologische und hydrographische Untersuchungen an zwei teichartigen Gewässer. *Beih. Bot. Centralbl. 51, 397—476.*

— 1935. Chemisch-biologische Untersuchungen an einem Teich. *Arch. Hydrobiol. 28, 619—658.*

— 1942. Zur Gliederung und Dynamik der Flachgewässer. *Arch. Hydrobiol. 38, 481—524.*

Wetzel, R. G., 1964. A comparative study of the primary productivity of higher aquatic plants, periphyton, and phytoplankton in a large, shallow lake. *Int. Revue ges. Hydrobiol. 49: 1, 1—61.*

Wright, R. T., 1964. Dynamics of a phytoplankton community in an ice-covered lake. *Limn. and Ocean. 9: 2, 163—178.*

IX. Tables

Table 1. Species list. (The 10 most important species or species groups in heavy type.)

CYANOPHYTA

Oscillatoria limosa Ag.
— *splendida* Grev.
— *Agardhii* Gom.
Lyngbya (*limnetica*)
Anabaena Scheremetievii Elenk.
— **flos-aquae** (Lyngb.) Bréb.

CHLOROPHYTA

a) *PROTOBLEPHARIDINAE*
Gyromitus cordiformis Skuja
b) *POLYMASTIGINAE*
Paramastix conifera Skuja
c) *EUCHLOROPHYCINAE*
Chlamydomonas cf. gloeopara Skuja
— sp.
Eudorina elegans E.
Volvox aureus E.
Gloeocystis planctonica (W. et G. S. West) Lemm.
— *bacillus* Teiling
Gloeococcus Schroeteri (Chod.) Lemm.
Characium gracilipes F. D. Lambert
Pediastrum duplex Meyen
— *Boryanum* (Turp.) Menegh.
Chlorella (*pyrenoidosa*)
Tetraëdron caudatum (Corda) Hansg.
— *incus v. gracillimum* Nauwerck
Scenedesmus bijugatus (Turp.) Kuetz.
— *bicellularis* Chod.
— *obliquus* (Turp.) Kuetz.

Dictyosphaerium elegans BACHMANN
— *Ehrenbergianum* NAEG.
Coelastrum microporum NAEG.
Selenastrum capricornutum PRINTZ
Ankistrodesmus falcatus (CORDA) RALFS
— *acicularis* A. BR.
— *setigerus* (SCHROED.) G. S. WEST
Coccomyxa sp.
Stichococcus minor NAEG. sec. CHOD.

d) *CONJUGATAE*
Closterium acutum v. variabile (LEMM.) KRIEGER
— *aciculare v. subpronum* W. et G. S. WEST
— *Ehrenbergii* MENEGH.
— *Kuetzingii* BRÉB.
Pleurotaenium trabecula (E.) NAEG.

EUGLENOPHYTA

Euglena cf. clavata SKUJA

CHRYSOPHYTA

a) *CHRYSOMONADINAE*
Chromulina cf. parva SKUJA
— **spp.**
Monochrysis aphanaster SKUJA
Chrysococcus minutus (FRITSCH) NYGAARD
Mallomonas akrokomos RUTTNER
— *caudata* IWANOFF
— (*tonsurata*)
Erkenia subaequiciliata SKUJA
Ochromonas spp.
Uroglena americana CALKINS
Pseudokephyrion Entzii CONRAD
— *sp.*
Stylochrysallis aurea (CHOD.) BACHM.
Dinobryon acuminatum RUTTNER
— *bavaricum* IMHOF
— *sociale v. stipitatum* (STEIN) LEMM.
— *divergens* IMHOFF
Bicoeca sp.

d) *DIATOMEAE*
Melosira islandica ssp. helvetica O. F. M.
Cyclotella (*comta*)
Rhizosolenia eriensis H. L. SMITH
Tabellaria fenestrata (LYNGB.) KUETZ.
— *flocculosa* (ROTH) KUETZ.
Diatoma elongatum (LYNGB.) AG.
Fragilaria construens (E.) GRUN.
Asterionella formosa HASSALL
Synedra (*acus*)
— *acus v. angustissima* GRUN.
— *ulna* (NITZSCH) E. (*v. danica*)
Surirella biseriata BRÉB.

c) *HETEROKONTAE*
Botryococcus Braunii KUETZ.

PYRROPHYTA

a) *CRYPTOMONADINAE*
Rhodomonas lacustris PASCHER et RUTTNER
— **minuta** SKUJA
Cryptomonas erosa E.
— **Marssonii** SKUJA
— *rostratiformis* SKUJA
Katablepharis ovalis SKUJA

b) *DINOPHYCINAE*
Amphidinium Lohammari SKUJA
Gymnodinium helveticum PENARD
— *sp.*
Peridinium (*bipes*)
— *pusillum* (PENARD) LEMM.

MYCOPHYTA

Cerasterias (=*Asterothrix*) *raphidioides* REINSCH

Table 2. The temporal variation at different sites of the most common phytoplankton species as cells · 10^4/l.

	17/6 1962					9/7 1962					29/7 1962				
	Sites					Sites					Sites				
	5	6	7	8	4	5	6	7	8	4	5	6	7	8	4
Oscillatoria splendida [1]	—	—	—	—	—	—	12	181	4	—	—	—	—	—	—
Anabaena Scheremetievii [1]	—	68	12	26	—	—	—	—	—	—	—	—	—	—	—
— *flos-aquae* [2]	0.92	0.81	0.86	0.88	0.14	—	—	—	—	—	—	—	—	—	0.01
Chlamydomonas spp.+ swarm spores	4	—	—	—	—	—	16	6.7	—	—	4.0	77	—	—	—
Characium gracilipes	—	—	—	—	—	—	5.4	—	—	—	—	—	—	—	—
Ankistrodesmus falcatus	83	150	80	120	44	27	—	11	2.7	9.4	6.7	2.7	—	—	—
"µ-*algae*"	2,400	5,600	11,000	8,300	4,500	4,300	4,300	12,000	8,500	5,900	4,500	2,100	2,500	4,200	3,500
"small monads"	600	630	450	1,000	470	120	47	130	170	170	97	170	180	210	140
"big monads"	23	47	16	63	6.7	2.7	13	23	27	17	9.7	6.7	18	6.7	17
Erkenia subaequiciliata	16	2.7	9.3	—	—	1.3	4.0	4.0	67	4.0	—	—	—	—	5.4
Dinobryon acuminatum	2.7	16	6.7	4.0	—	—	—	—	—	—	—	—	—	—	—
Rhodomonas lacustris	6.7	4.0	2.7	8.0	4.0	6.7	—	11	6.7	5.4	—	5.4	2.7	4.0	—
— *minuta*	47	23	43	69	110	20	51	60	17	71	7.0	54	18	—	150
Cryptomonas Marssonii	1.3	1.3	2.7	15	6.7	—	—	2.7	—	—	0.2	1.0	0.3	0.1	0.2
Katablepharis ovalis	45	25	39	48	27	—	—	1.3	4.0	13	—	4.0	6.7	—	20
"small *Gymnodales*"	4.0	9.3	4.0	4.0	2.7	—	—	—	—	—	—	2.7	2.7	—	6.7

	29/7 1962 at site 6 at the following depths				27/8 1962					18/9 1962				
					Sites					Sites				
	0.1 m	0.3 m	0.5 m	1.0 m	5	6	7	8	4	5	6	7	8	4
Oscillatoria splendida [1]	20	26	32	159	—	2	22	57	—	—	—	—	62	11
Anabaena Scheremetievii [1]	—	—	—	—	—	—	—	—	—	—	—	—	—	—
— *flos-aquae* [2]	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chlamydomonas spp.+ swarm spores	100	110	91	71	—	1,600	2,100	8,800	380	8.0	94	83	52	67
Characium gracilipes	—	—	—	—	—	13	8.0	6.7	1.3	—	—	—	—	—
Ankistrodesmus falcatus	—	—	—	—	—	—	—	—	—	—	—	—	—	—
"µ-algae"	1,900	2,300	2,500	2,700	3,200	1,100	1,000	1,100	1,200	530	1,100	600	870	1,500
"small monads"	100	280	150	77	150	150	760	100	210	150	260	370	320	870
"big monads"	4.0	13	5.4	2.7	6.7	39	9.3	16	48	13	29	27	33	110
Erkenia subaequciliata	—	—	—	—	2.7	—	—	—	—	2.7	—	—	—	—
Dinobryon acuminatum	—	—	—	—	—	—	—	2.7	—	—	—	—	—	—
Rhodomonas lacustris	5.4	16	5.4	5.4	4.0	60	21	17	21	—	—	—	—	—
— *minuta*	44	36	33	40	11	170	60	2.7	64	28	73	51	84	49
Cryptomonas Marssonii	0.4	0.7	0.6	1.1	0.7	5.4	2.7	5.4	5.4	6.7	2.7	11	17	15
Katablepharis ovalis	—	1.3	2.7	2.7	6.7	6.7	6.7	13	13	—	11	6.7	16	17
"small *Gymnodales*"	—	2.7	4.0	1.3	—	5.4	—	5.3	1.3	—	—	—	—	14

---

[1] Trichomes, cm.

[2] Colonies, diameter c. 250 µ.

Table 3 a. Composition of phytoplankton as volume/l at different sites and times.

	Site 5		Site 6		Site 7		Site 8		Site 4		Mean of sites 4—8	
	$\mu^3 \cdot 10^6$	%	$\mu^3 \cdot 10^6$	%	$\mu^3 \cdot 10^6$	%	$\mu^3 \cdot 10^6$	%	$\mu^3 \cdot 10^6$	%	$\mu^3 \cdot 10^6$	%
17/6 1962												
Cyanophyta	138	10	122	7	129	8	134	5	21	2	109	7
Chlorophyta	339	25	655	38	754	48	726	30	338	30	562	34
Chrysomonadinae	688	50	789	46	530	33	1,201	50	511	46	744	45
Diatomeae	30	2	15	1	5	—	2	—	—	—	10	1
Cryptomonadinae	167	12	96	5	155	10	335	14	241	21	199	12
Dinophycinae	20	1	47	3	20	1	20	1	14	1	24	1
Total	1,382	100	1,724	100	1,593	100	2,418	100	1,125	100	1,648	100
Netplankton of total	168	12	136	8	135	9	136	6	21	2	119	7
9/7 1962												
Cyanophyta	2	—	3	1	6	1	+	—	—	—	2	—
Chlorophyta	291	64	268	61	635	66	432	57	319	48	389	59
Chrysomonadinae	128	28	82	19	190	20	278	37	215	32	178	27
Diatomeae	2	—	15	3	1	—	—	—	6	1	5	1
Cryptomonadinae	38	8	53	12	117	12	42	5	111	17	72	11
Dinophycinae	—	—	20	4	5	1	8	1	16	2	10	2
Total	461	100	441	100	954	100	760	100	666	100	656	100
Netplankton of total	5	1	21	5	6	1	+	—	6	1	8	1
28/7 1962												
			cf. table 3 b.									
Cyanophyta	—	—	—	—	—	—	—	—	2	—	+	—
Chlorophyta	248	63	189	40	125	31	212	47	176	31	190	42
Chrysomonadinae	121	31	187	40	225	57	227	51	186	32	189	41
Diatomeae	14	4	—	—	—	—	—	—	—	—	3	1
Cryptomonadinae	9	2	86	18	41	10	11	2	192	33	68	15
Dinophycinae	—	—	8	2	8	2	—	—	20	4	7	2
Total	392	100	470	100	399	100	450	100	576	100	457	100
Netplankton of total	2	—	—	—	—	—	2	—	2	—	1	—
27/8 1962												
Cyanophyta	+	—	+	—	1	—	6	—	—	—	1	—
Chlorophyta	167	40	292	30	309	52	996	78	145	21	382	48
Chrysomonadinae	173	41	271	28	132	22	140	11	340	49	211	27
Diatomeae	38	9	6	—	+	—	—	—	1	—	9	1
Cryptomonadinae	43	10	387	40	153	26	125	10	197	29	181	23
Dinophycinae	+	—	16	2	—	—	19	1	4	1	8	1
Total	421	100	972	100	595	100	1,286	100	687	100	792	100
Netplankton of total	+	—	1	—	1	—	9	1	+	—	2	—
18/9 1962												
Cyanophyta	—	—	—	—	—	—	3	—	+	—	1	—
Chlorophyta	42	10	90	16	81	11	79	12	176	11	94	12
Chrysomonadinae	190	44	343	62	442	62	405	63	1,148	72	505	64
Diatomeae	80	19	—	—	—	—	1	—	—	—	16	2
Cryptomonadinae	117	27	122	22	193	27	159	25	238	15	166	21
Dinophycinae	1	—	—	—	—	—	—	—	42	2	9	1
Total	430	100	555	100	716	100	647	100	1,604	100	791	100
Netplankton of total	86	20	—	—	+	—	5	1	2	—	19	2

Table 3 b. Composition of phytoplankton as volume/l on 28/7 1962 at site 6. Vertical distribution.

	0.1 m		0.3 m		0.5 m		1.0 m		Mean of 0.1—1.0 m	
	$\mu^3 \cdot 10^6$	%	$\mu^3 \cdot 10^6$	%	$\mu^3 \cdot 10^6$	%	$\mu^3 \cdot 10^6$	%		
Cyanophyta	1	—	2	—	1	—	7	2	3	1
Chlorophyta	195	53	226	36	219	48	206	55	211	46
Chrysomonadinae	110	30	313	49	164	36	84	23	167	37
Diatomeae	1	—	—	—	—	—	1	—	+	—
Cryptomonadinae	61	17	86	14	58	13	70	19	69	15
Dinophycinae	—	—	8	1	12	3	4	1	6	1
Total	368	100	635	100	454	100	372	100	456	100
Netplankton of total	1	—	2	—	5	1	8	2	4	1

Table 4. Dark-assimilation values as mg C/m³ · d.

Depth m	Site 4						Site 6
	0.1	0.5	0.7	1.0	2.0	2.2	1.0
1961:							
1/11	1.4	—	—	1.0	—	—	—
1962:							
26/1	—	0.3	—	—	0.2	—	—
13/3	—	—	—	—	0.2	—	—
9—10/4	—	—	1.3	—	—	1.1	—
17—18/6	4.4	—	—	—	6.8	—	—
9—10/7	5.3	—	—	—	4.8	—	5.7
28—29/7	5.9	—	—	—	—	7.7	—
27—28/8	5.8	—	—	—	—	2.7	—
18—19/9	4.1	—	—	—	—	4.0	—
24—25/10	2.1	—	—	—	—	2.2	—

Table 5. The efficiency of assimilation stated as the ratio of primary production (P) in mg C/m² · d to standing crop of phytoplankton (TV) in mm³/m³.

1962:	Site 5			Site 6			Site 7			Site 8			Site 4			Mean of sites 4—8		
	P	TV	P:TV	P	TV	P:TV	P	TV	P:TV	P	TV	P:TV	P	TV	P:TV	P	TV	P:TV
17/6–18/6	125	1,382	0.09	262	1,724	0.15	181	1,593	0.11	280	2,418	0.12	279	1,125	0.25	225	1,648	0.14
9/7–10/7	233	461	0.51	142	441	0.32	138	954	0.14	113	760	0.15	263	666	0.39	178	656	0.27
28/7–29/7	49	392	0.13	96	470	0.20	177	399	0.44	111	450	0.25	274	576	0.48	141	457	0.31
28/7–29/7[1]				72[1]	456[1]	0.16[1]												
27/8–28/8	55	421	0.13	198	972	0.20	80	595	0.13	80	1,286	0.06	167	687	0.24	116	792	0.15
18/9–19/9	86	430	0.20	26	555	0.05	56	716	0.08	82	647	0.13	117	1,604	0.07	73	791	0.09

[1] Extra series, cf. p. 143, Fig. 5 b on p. 153, and Table 3 b above.

Liver and muscle glycogen and blood lactate in hatchery-reared *Salmo salar* L. following exercise in winter and summer

By Curt Wendt *

Salmon Research Laboratory, Älvkarleö, and Institute of Zoophysiology,
University of Gothenburg, Gothenburg, Sweden

Introduction

Fish are considered to have low glycogen reserves as compared with mammals (Black *et al.*, 1960). Nevertheless there occur a great accumulation of lactate both in the muscle and in the blood following hard muscular exercise (von Buddenbrock, 1938, Secondat and Diaz, 1942; Black, 1955, 1957 a, b, c; Leivestad *et al.*, 1957; Nakatani, 1957; Parker and Black, 1959; Parker *et al.*, 1959; Miller *et al.*, 1959, 1962; Black *et al.*, 1959, 1960, 1962; Heath and Pritchard, 1962; Caillouet, Jr., 1964; Dean and Goodnight, 1964; Wendt, 1964 a, b, c;). The source of lactate seems to be muscle glycogen (Black *et al.*, 1960). The blood lactate continues to rise after exercise for 2—4 hours and the decline to preexercise level is slow as compared with mammals. Sometimes significant mortality has appeared in connection with high blood lactate values (Secondat and Diaz, 1942; Black, 1957 c; Miller, 1958; Parker and Black, 1959; Parker *et al.*, 1959).

The aim of the present investigation was to study the effect of exercise and temperature on liver and muscle glycogen and blood lactate in hatchery-reared salmon (*Salmo salar* L.). As reported earlier for *Salvelinus fontinalis,* lower blood lactate values appeared after exercise at 5°C than at 15°C, and it seemed necessary to standardize the method of exercise (Wendt, 1964 b).

Material and methods

The experiments were carried out at the Salmon Research Laboratory, Älvkarleö, Sweden, on hatchery-reared Salmon (*Salmo salar* L.) from the River Lule Älv. Two-year-olds were used during February—March 1964 (11.2—19.2; 4.3—12.3), and 1 $^{1}/_{2}$-year-olds during August 1964 (6.8—12.8).

When 12 months old, after being fed on a raw diet [1] (2 days a week) and pellets [2] (4 days a week) for the last 6 months, the 2-year-old salmon were graded (average weight 32.9 g) and from October 16, fed on pellets only. The

---

[1] 10 % liver, 40 % spleen, 25 % fish, 20 % prawns, and 5 % kelp meal.

[2] 47.6 % protein, 4.9 % fat, 29.1 % nitrogen free extract, 1.5 % fibre, 10.4 % ash, and 5 % water.

* Present address: Kgl. Fiskeristyrelsen, Fack, Göteborg 5, Sweden.

1 1/2-year-old salmon were not graded and were given pellets [2] from May 26. Previously they had a raw diet [3] 2 days a week and pellets [2] 4 days a week. Both batches were kept in 11.5 m^2 troughs in the Trough hall (CARLIN, 1963), and were fed during summer 4 times a day except on Saturdays (twice daily) and Sundays (once daily). As the water cooled, the food consumption decreased, and the fish examined in February—March were fed once a day, except on Saturdays and Sundays, from October 16, 1963.

Before testing, the fish were transferred to covered dark basins and kept without feeding for 18—22 hours.

The fishes were exercised to exhaustion in an exercising apparatus and left to recover there. The recovery took place without feeding. The apparatus, designed primarily by HEATH and PRITCHARD (1962), was somewhat modified. It was entirely closed with the exception of an opening in the lid giving access to a short cylinder for inserting the fish. The lid was easily removable. A repulsion motor (1/10 h.p., 50 per., 2800—0—2800 r.p.m.) drove the stainless-steel propeller. At both ends of the swimming chamber (440×125 mm) stainless-steel wirenetting was applied, and another net was placed obliquely along the chamber to keep the fish out of the backwater. Immediately in front of the rear wirenetting were mounted two aluminium electrodes to deliver shocks (4 v; 50 cycles). A 3-foot Perspex column was arranged to permit water at a constant rate (1 litre/min).

Ordinary hatchery water supplied the troughs, basins and apparatus. The water temperature during February—March was 0.2°C, and oxygen saturation ranged from 80 to 85 %. During August the values were from 97 to 100 %. The pH fluctuated during both periods between 6.8 and 7.3. Dissolved oxygen and pH were determined as described in WENDT (1964 b).

In February—March one group of fishes was acclimatized to 11.5°C. It was kept without feeding in a plastic trough (0.9 m^2) supplied with aerated hatchery water, which was gradually heated to 11.5°C during 10 days, at which temperature they were held for another 14 days before being exercised. A control group was treated in the same way without any increase of the water temperature.

Individual fishes were sampled before exercise, after exercise, and at different times during recovery. The fish was stunned with a blow on the head and quickly placed, ventral side up, in a V-shaped trough immersed in water, thus permitting respiratory movements. In contrast to earlier experiments, no anaesthetic was used, (WENDT, 1964 b). Blood was drawn from the heart into a heparin-rinsed syringe and immediately deproteinized in trichloroacetic acid (TCA) before the fish was killed for subsequent sampling of muscle and liver.

0.1 ml blood was ejected into 1 ml 5 % TCA and centrifuged at 2500 r.p.m. for 10 minutes. The protein-free fluid was stored in glass ampules at 5°C for

---

[3] 30 % liver, 40 % spleen, and 30 % prawns.

about a month until it was analysed for lactic acid (SCHOLANDER and BRADSTREET, 1962).

Muscle samples (about 0.2 g) were taken from the epaxial muscle just in front of and below the dorsal fin. In most cases the whole liver was excised for liver glycogen determinations. Muscle samples as well as liver samples were immediately placed directly into a mixture of solid carbon dioxide (dry ice) and 95 ⁰/₀ alcohol. After the removal of scale and skin in the frozen state, the samples were stored for 2—3 hours on dry ice until they were weighed in pre-weighed centrifuge tubes containing 30 ⁰/₀ KOH, and immediately boiled for 15 minutes in a water bath. The digests were stored at room temperature for several months without significant changes before analysing. Muscle and liver glycogen were determined according to MONTGOMERY (1957), but instead of filtering the diluted glycogen solutions these were centrifuged to remove interfering material (ROE *et al.,* 1961).

Blood and tissue samples were taken from the same fish in order to see the relations within a fish. When comparing different groups, one fish from each group was examined on the same occasion.

The weight and standard length (LAGLER, 1959) were recorded and the coefficient of condition (K) was calculated according to $\frac{100 \times W}{L^3}$ (BROWN, 1957).

Results

A. Methodology

As shown in Table 1, it was necessary to keep the fish undisturbed for 18—22 hours in dark basins in order to ensure an unexercised condition. Without this treatment, higher blood lactate values were recorded, especially in August, but muscle and liver glycogen values remained about the same.

Table I. Liver and muscle glycogen in hatchery-reared *Salmo salar* L. after 18—22 hours of rest (a), and immediately after being taken out of the trough (b). $\left(\mathrm{SD} = \pm \sqrt{\frac{S(x-\bar{x})^2}{n-1}}\right)$

		0.2°C Feb. 1964		15°C Aug. 1964	
		a	b	a	b
Liver	Mean ± SD	1.14 ± 1.36	0.61 ± 0.48	3.85 ± 1.11	4.24 ± 1.48
Glycogen	(n)	(6)	(8)	(10)	(5)
(g ⁰/₀)	Range	0.11—3.06	0.16—1 60	2.01—5.22	2.38—5.94
Muscle	Mean ± SD	0.168 ± 0.093	0.157 ± 0.059	0.593 ± 0.148	0.502 ± 0.239
Glycogen	(n)	(6)	(8)	(10)	(5)
(g ⁰/₀)	Range	0.034—0.272	0.108—0.285	0.359—0.806	0.292—0.772
Blood	Mean ± SD	3.5 ± 2.1	7.5 ± 5.8	14.6 ± 5.7	49.3 ± 14.0
Lactate	(n)	(6)	(8)	(8)	(5)
(mg ⁰/₀)	Range	2—7	2—18	7—24	31—52

Table II. Comparison of muscle-glycogen levels in muscle pieces taken from the epaxial muscle just in front of and below the dorsal fin on one side of the fish (a) with those taken from the other side including the lateral line (b). Unexercised hatchery-reared *Salmo salar* L. July 1963.

a	b
0.527	0.938
0.436	0.605
0.387	0 407
0.326	0.537
0.124	0.198
0.102	0.165
0.300 ± 0.170[1]	0.475 ± 0.284

[1] Mean ± SD.

The fishes were exercised to exhaustion in an exercising apparatus. For purposes of comparison some fishes were chased by hand for 15 minutes. In February-March the latter showed lower blood lactate and higher muscle glycogen levels than the former. In August, however, there was a tendency to higher blood lactate levels in the hand-chased fishes and several were moribund when sampled after 2—4 hours. (Results will be published later.)

Results of a comparison of muscle glycogen in small pieces taken from the epaxial muscle just in front of and below the dorsal fin on one side of the fish (a) with those from the other side including the lateral line (b) are presented in Table II. Higher levels, about 50 %, were obtained in the latter; this may have been due to a contamination with the red muscle. As shown by Buttkus (1963) the sarcoplasmic area of the red muscle of lingcod (*Ophiodon elongatus*) contained more glycogen than that of the white muscle.

With few exceptions, sampling was completed within 3 minutes. No exact recordings were made, but, as shown by Black (1957 a) and Black *et al.* (1960) in trout, there seemed to be no significant rise in blood lactate or autolysis of glycogen up to 4 minutes after capture.

B. Behaviour during exercise

One at a time all the fish were exercised to the point of exhaustion in the apparatus in the same way. After netting the fish was quickly inserted in the swimming chamber with a slight water current, which made it easier for it to orientate itself. The current was gradually increased to about 0.75 m/sec[1] (in the middle of the swimming chamber) after 5 minutes, and further to about 1 m/sec after 10 minutes. Most of the fishes were now swim-

---

[1] Determined according to Pitot ($v=0.99\sqrt{2gh}$).

ming at a steady rate at the bottom of the apparatus, but in August single fishes could not breast the current for any length of time, and a few were not able to withstand 1 m/sec at any time. Often they did not find a position but, thanks to the repulsion motor, it was possible to reverse the water current. Thus it was not necessary to use shocks at every moment, when the fish sometimes struggled against the net. On the other hand some fish were not exhausted within 60 minutes. When the fish became tired it left the bottom, lost its headway, and soon afterwards even a slight water current caused it to fall back against the wirenetting, and electrical shocks could not stimulate it to further work. After exercise, the fatigued fish remained motionless until sampled. In February—March (0.2°C.) fatigue occurred after 32 ± 8.1 (48) minutes and in August (15°C.) after 21 ± 5.2 (34) minutes. A group of starved fishes (February—March) was exhausted after 35 ± 11.0 (9) minutes, and in another group, acclimatized from 0.2°C. to 11.5°C. and starved, only 3 of 8 were exhausted within 60 minutes (Table VIII).

C. Unexercised, exercised and recovery states
Temp. 0.2°C. February—March 1964

Coefficient of condition. Body weights and standard lengths are given in Table IV. The overall coefficient of condition for the 55 fishes used was 1.143, with a range between the different groups of 1.109—1.188.

Liver glycogen. The average unexercised level of liver glycogen was 1.40 g % (Tab. IV). When calculated separately for each month the level rose from 0.64 g % in February to 1.93 g % in March, an increase closely related to the change in another pellet-fed group (Wendt, 1964 c).

Exercise seemed to cause a decrease, while the recovery values fluctuated (Fig. 1); but owing to the great deviation it is doubtful whether there were any real differences. In addition, there occurred a few pale livers both in males and in females.

Precocious males sampled in February had considerably more liver glycogen than the immature ones (Table III), and the liver appeared pale.

Table III. Unexercised levels of liver and muscle glycogen in 2-year-old precocious and immature males of hatchery-reared *Salmo salar* L. Feb. 1964. Temp. 0.2°C.

	Precocious	Immature
Liver Glycogen (g %)	4 46	1.60
	3.42	1.02
	2.53	0.34
Muscle Glycogen (g %)	0.780	0.285
	0.384	0.189
	0.234	0.115

Muscle glycogen. As in liver glycogen, there was an increase in the unexercised level of muscle glycogen from February to March, from an average of 0.168 g % to 0.233 g %, with an overall average level for both months of 0.190 g % (Table IV; Fig. 1).

As a whole, exercise caused a significant decrease (t-test, $P < 0.001$), but not quite significant at the $P = 0.01$ level when comparing values from February only. The loss, however, was 76 % and 71 % respectively.

Recovery during 15 hours caused no significant increase in muscle glycogen. There was a tendency to a somewhat higher level at the end of the recovery period.

Just as in the liver, higher glycogen levels were recorded in the muscles of precocious males (Table III).

Blood lactate. The unexercised average level was 3.3 mg %. This increased to 38.8 mg % at the cessation of exercise (Table IV; Fig. 1), which was closely related to 40.6 mg % obtained after 19 minutes of exercise in November 1963 at 4°C (WENDT, 1964 a). Blood lactate still increased for some time during the recovery. The highest values appeared after 2—4 hours. Not even after 15 hours was the unexercised level reached.

Temp. 15°C. August 1964

Coefficient of condition. Body weights and standard lengths are presented in Table V. In all, 42 fishes were used and they showed an overall coefficient of condition of 1.234, with a range between the different groups of 1.218—1.257.

Liver glycogen. The unexercised average level, 3.85 g %, was significantly higher than in February—March ($P < 0.001$). There was a tendency to a lower level after exercise, but the difference was not significant (Tab. V; Fig. 2). During the recovery the level fluctuated and, as said above, it is doubtful if any real differences existed. As in February—March, a few pale livers appeared in both sexes.

Muscle glycogen. As in liver, the average glycogen level was higher in August, being about 3 times that in February—March (Table VI). The obtained values were somewhat higher than those recorded in July, 1963, in 1 $^1/_2$-year-old salmon fed the mixed diet (WENDT, 1964 a).

Exercise caused a significant fall in muscle glycogen ($P < 0.001$). The exercised average level (0.299 g %) was about half that of the unexercised one (0.593 g %). During the recovery the level fluctuated just as in liver glycogen (Fig. 2).

Blood lactate. The average unexercised level of 14.6 mg % was about 4 times that in February—March, but somewhat lower than in July 1963 (WENDT, 1964 a). Following exercise to exhaustion the average level rose

Table IV. Body weights, standard lengths and levels of liver and muscle glycogen and blood lactate after exercise to exhaustion and during post-exercise recovery in hatchery-reared *Salmo salar* L. February—March 1964. Temp. 0.2°C. $\left(\mathrm{SD} = \pm \sqrt{\frac{S(x-\bar{x})^2}{n-1}}\right)$

				Recovery from exercise				
		Unexercised	Exercised 29±5.1[1]	1 hour (33±6.5)	2 hours (30±6.1)	4 hours (34±6.4)	6 hours (36±7.4)	15 hours (36±5.5)
Body Weight (grams)	Mean±SD	40±7.3	39±5.5	38±2.9	40±3.7	41±3.8	45±5.1	39±1.5
	(n)	(9)	(11)	(8)	(10)	(7)	(5)	(6)
	Range	35—57	34—47	33—41	33—45	36—47	38—50	36—42
Standard Length (cm)	Mean±SD	15.19±1.02	15.09±0.67	14.73±0.41	15.24±1.25	15.18±0.45	15.95±0.37	15.13±0.37
	(n)	(8)	(10)	(8)	(10)	(8)	(5)	(6)
	Range	14.3—17.3	14.3—16.0	14.2—15.2	14.7—15.8	14.5—15.8	15.5—16.5	14.5—15.6
Liver Glycogen (g %)	Mean±SD	1.40±1.37	0.44±0.63	1 07±0.87	1.30±1.28	0 83±0.69	0.86±0.58	0.44±0.30
	(n)	(9)	(11)	(8)	(9)	(8)	(5)	(6)
	Range	0.11—3.62	0.05—1.89	0.20—2.46	0.09—2.73	0.19—2.03	0.10—1.61	0.12—0.90
Muscle Glycogen (g %)	Mean±SD	0.190±0.089	0.045±0.047	0.088±0.031	0.061—0.029	0.070±0.049	0.098±0.048	0.111±0.027
	(n)	(9)	(11)	(8)	(9)	(8)	(5)	(6)
	Range	0.034—0.320	0.009—0.177	0.036—0.129	0.022—0.124	0.023—0.172	0.035—0.143	0.074—0.149
Blood Lactate (mg %)	Mean±SD	3.3±1.7	38 8±13.3	44.9±9.0	57.1±18.3	57.3±26.7	44.6±28.4	18.3±15.2
	(n)	(9)	(11)	(8)	(10)	(8)	(5)	(6)
	Range	2—7	17—56	39—57	32—85	14—95	22—87	4—47

[1] Exercising mean ± SD in minutes.

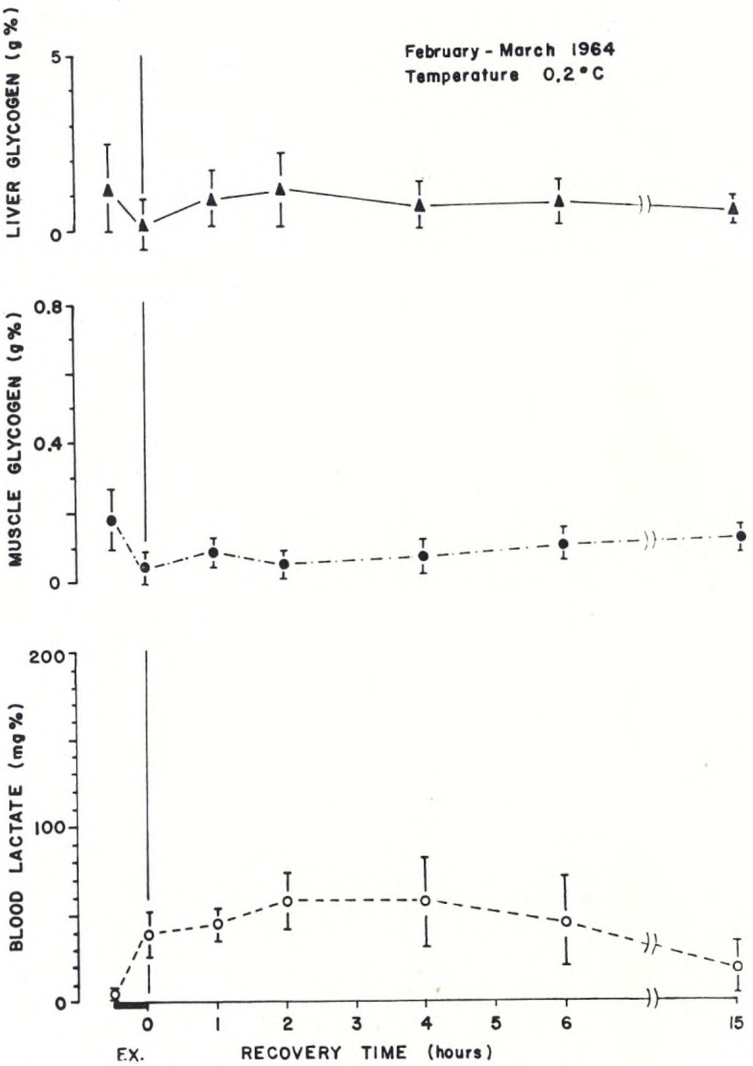


Fig. 1. Changes in liver and muscle glycogen and blood lactate after exercise to exhaustion and during post-exercise recovery in hatchery-reared *Salmo salar* L. February—March 1964. Temp. 0.2°C.

to 76.3 mg % simultaneously with a significant fall in muscle glycogen. The highest values were recorded after 2 hours of recovery. One fish was moribund when sampled after 4 hours and had 130 mg % blood lactate. After 15 hours of recovery the level was somewhat higher than the unexercised level.

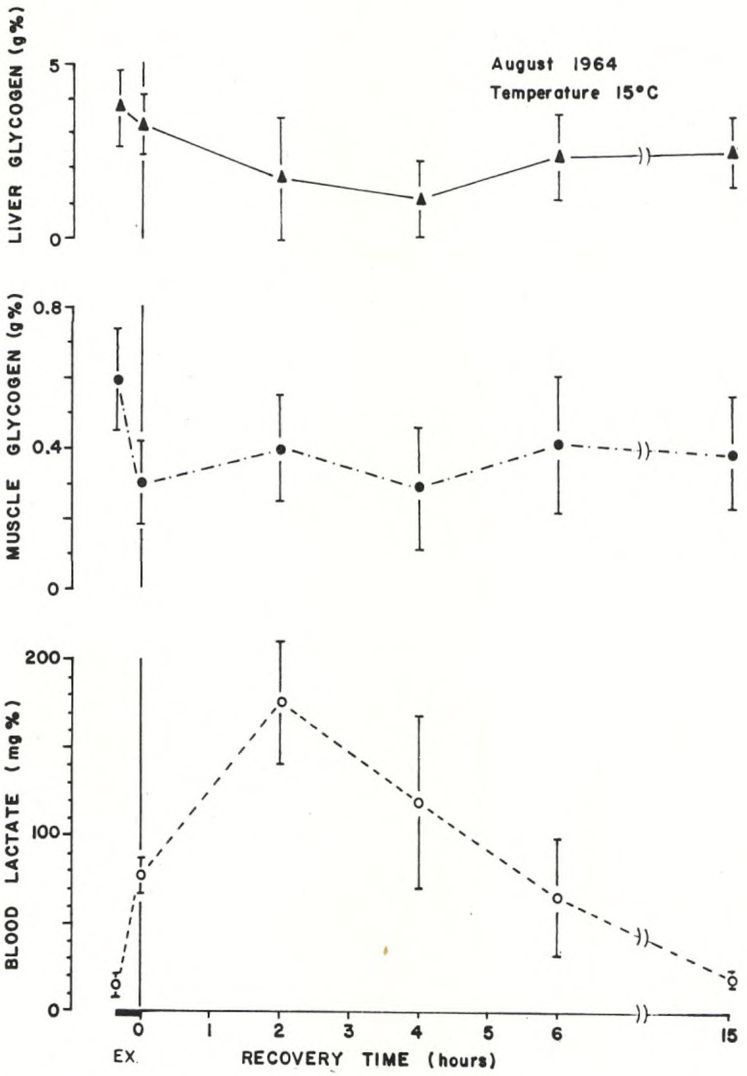


Fig. 2. Changes in liver and muscle glycogen and blood lactate after exercise to exhaustion and during post-exercise recovery in hatchery-reared *Salmo salar* L. August 1964. Temp. 15°C.

D. Influence of starvation
Temp. 0.2°C. February—March 1964

There seemed to be no difference between the fed batch and the unfed one. (Tab. IV and VI). Coefficients of condition were 1.143 and 1.134 respectively. Liver glycogen fluctuated but was not lower after starvation than before.

Table V. Body weights, standard lengths and levels of liver and muscle glycogen and blood lactate after exercise to exhaustion and during post-exercise recovery in hatchery-reared *Salmo salar* L. August 1964. Temp. 15°C.

$$\left(\mathrm{SD} = \pm \sqrt{\frac{S(x-\bar{x})^2}{n-1}} \right)$$

				Recovery from exercise			
		Unexercised	Exercised 20 ± 6.1[1]	2 hours (21 ± 4.6)	4 hours (23 ± 5.6)	6 hours (19 ± 3.8)	15 hours (21 ± 6.1)
Body	Mean ± SD	27.5 ± 11.8	25.2 ± 4.0	26.4 ± 5.6	32.8 ± 8.1	26.3 ± 2.5	26.5 ± 6.4
Weight	(n)	(10)	(8)	(7)	(6)	(5)	(7)
(grams)	Range	16—56	19.5—30.0	21.5—36.5	22.0—41.0	24.0—30.5	19.5—39.0
Standard	Mean ± SD	13.09 ± 1.67	12.70 ± 0.70	12.94 ± 0.76	13.78 ± 0.84	12.84 ± 0.35	12.91 ± 1.00
Length	(n)	(10)	(8)	(7)	(5)	(5)	(7)
(cm)	Range	11.0—16.7	11.6—13.5	12.4—14.5	13.0—14.8	12.5—13.4	12.0—14.9
Liver	Mean ± SD	3.85 ± 1.11	3.32 ± 0.93	1.80 ± 1.79	1.23 ± 1.10	2.41 ± 1.22	2.56 ± 1.0
Glycogen	(n)	(10)	(7)	(7)	(6)	(4)	(7)
(g %)	Range	2.01—5.22	2.45—5.12	0.20—4.37	0.20—3.03	0.62—3.37	0.94—3.87
Muscle	Mean ± SD	0.593 ± 0.148	0.299 ± 0.122	0.397 ± 0.151	0.288 ± 0.167	0.406 ± 0.190	0.379 ± 0.165
Glycogen	(n)	(10)	(7)	(7)	(6)	(4)	(7)
(g %)	Range	0.359—0.806	0.117—0.436	0.261—0.706	0.121—0.596	0.260—0.672	0.080—0.556
Blood	Mean ± SD	14.6 ± 5.7	76.3 ± 9.9	175.4 ± 35.0	119.0 ± 48.8	65.2 ± 32.8	21.0 ± 3.5
Lactate	(n)	(8)	(7)	(7)	(5)	(5)	(6)
(mg %)	Range	7—25	58—85	127—221	73—191	21—111	16—26

---

[1] Exercising mean ± SD in minutes.

Table VI. Body weights, standard lengths, liver and muscle glycogen and blood lactate before and after exercise to exhaustion and after 2 hours of recovery in hatchery-reared *Salmo salar* L. starved for 25 days at 0.2°C. February—March 1964. $\left(\mathrm{SD} = \pm \sqrt{\frac{S(x-\bar{x})^2}{n-1}}\right)$

				Recovery
		Unexercised	Exercised 33 ± 7.0[1]	2 hours (34 ± 16.2)
Body Weight (grams)	Mean ± SD	37.8 ± 7.5	36.3 ± 7.7	38.5 ± 6.5
	(n)	(4)	(6)	(4)
	Range	28—46	30—51	31—45
Standard Length (cm)	Mean ± SD	14.70 ± 1.00	14.93 ± 0.99	15.03 ± 0.92
	(n)	(4)	(6)	(4)
	Range	13.6—16.0	13.8—16.7	14.0—15.8
Liver Glycogen (g %)	Mean ± SD	3.70 ± 0.56	2.10 ± 0.66	1.98 ± 0.89
	(n)	(3)	(6)	(4)
	Range	2.94—4.71	1.25—2.88	0.96—2.85
Muscle Glycogen (g %)	Mean ± SD	0.224 ± 0.073	0.073 ± 0.038	0.136 ± 0.048
	(n)	(4)	(6)	(4)
	Range	0.171—0.325	0.038—0.136	0.068—0.181
Blood Lactate (mg %)	Mean ± SD	6.3 ± 2.1	35.4 ± 10.2	56 5 ± 14.0
	(n)	(3)	(5)	(4)
	Range	4—8	22—49	45—76

[1] Exercising mean ± SD in minutes.

Table VII. Body weights, standard lengths, liver and muscle glycogen and blood lactate in unexercised hatchery-reared *Salmo salar* L. starved for 6 and 21 days at 15°C. August 1964. $\left(\mathrm{SD} = \pm \sqrt{\frac{S(x-\bar{x})^2}{n-1}}\right)$

		Fed	Starved	
			6 days	21 days
Body Weight (grams)	Mean ± SD	27.5 ± 11.8	27.8 ± 5.8	24.2 ± 4.2
	(n)	(10)	(4)	(5)
	Range	16—56	20.5—33.5	18—29
Standard Length (cm)	Mean ± SD	13.09 ± 1.67	13.63 ± 0.95	13.54 ± 0.89
	(n)	(10)	(4)	(5)
	Range	11.0—16.7	12.4—14.5	12.1—14.5
Liver Glycogen (g %)	Mean ± SD	3.85 ± 1.11	1.35 ± 0.16	0.67 ± 0.37
	(n)	(10)	(4)	(5)
	Range	2.01—5 22	1.14—1.51	0.51—1.25
Muscle Glycogen (g %)	Mean ± SD	0.593 ± 0.148	0.189 ± 0.048	0.089 ± 0.026
	(n)	(10)	(4)	(5)
	Range	0.359—0.806	0.135—0.252	0.046—0.123
Blood Lactate (mg %)	Mean ± SD	14.6 ± 5.7	14.3 ± 7.3	18.3 ± 7 6
	(n)	(8)	(4)	(5)
	Range	7—24	5—21	9—25

Muscle glycogen was about the same in both the fed and the starved group. There was no difference in blood lactate between the two groups at the cessation of exercise or after 2 hours of recovery. A higher unexercised level was recorded in the starved batch, which was probably due to direct sampling without retention in dark basins.

15°C. August 1964

As shown in Table VII 6 days of starvation caused a significant decrease ($P < 0.001$) in liver and muscle glycogen. The coefficient of condition decreased from 1.257 to 1.098. No difference, however, were obtained in blood lactate. 21 days of starvation caused a further decline in the glycogen levels and likewise in the coefficient of condition to 0.974. No significant difference appeared in blood lactate.

E. Effect of acclimatization to higher temperature
From 0.2°C to 11.5°C.

The fish were acclimatized without feeding. Compared with the starved control group (Table VI) the overall coefficient of condition decreased from 1.14 to 1.06. Liver glycogen decreased to an unexercised average level of

Table VIII. Body weights, standard lengths, liver and muscle glycogen and blood lactate before and after exercise to exhaustion and after 2 hours of recovery in hatchery-reared *Salmo salar* L. acclimatized from 0.2°C to 11.5°C. February—March 1964. $\left(\mathrm{SD} = \pm \sqrt{\frac{S(x-\bar{x})^2}{n-1}}\right)$

				Recovery
		Unexercised	Exercised[1]	2 hours[2]
Body	Mean ± SD	37.7 ± 8 6	39.0 ± 1.0	35.8 ± 4.4
Weight	(n)	(6)	(3)	(5)
(grams)	Range	26—45	38—40	32—39
Standard	Mean ± SD	15.08 ± 0.96	15.56 ± 0.81	15.08 ± 0.56
Length	(n)	(6)	(3)	(5)
(cm)	Range	14.2—16.4	15.2—16.5	14.5—15.7
Liver	Mean ± SD	0.82 ± 0.28	0.35 ± 0.05	0.17 ± 0.068
Glycogen	(n)	(6)	(3)	(5)
(g %)	Range	0.55—1.17	0.29—0.38	0.12—0.29
Muscle	Mean ± SD	0.220 ± 0.057	0.138 ± 0.019	0.154 ± 0.090
Glycogen	(n)	(6)	(3)	(5)
(g %)	Range	0.125—0 276	0.117—0.153	0.045—0.250
Blood	Mean ± SD	8.5 ± 4.0	40.7 ± 16.2	42.8 ± 37.2
Lactate	(n)	(6)	(3)	(5)
(mg %)	Range	5—16	26—58	16—148

[1] Exercised for 60, 57, and 60 minutes.

[2] Exercised for 60, 59, 60, 56, and 60 minutes.

0.82 g ⁰/₀, while the muscle glycogen level was maintained (Table VII). Exercise and recovery seemed to cause a progressive decline in liver glycogen, but there was large deviation. A long period of exercise was needed, and of eight fishes only three were exhausted within 60 minutes. There was only a tendency to lower muscle glycogen values at exhaustion. An average unexercised blood lactate level of 8.5 mg ⁰/₀ rose to 40.7 mg ⁰/₀ following exercise, and there seemed to be no further increase during recovery. If the high value 148 mg ⁰/₀ is excluded, the average value after 2 hours of recovery change to 16.5 mg ⁰/₀.

Unfortunately the acclimatized group contained several precocious males, which had to be excluded and therefore only a few experiments were performed.

Discussion

Diet and feeding frequency play an important role among factors known to influence glycogen stores in fish, (MILLER *et al.*, 1959; BLACK *et al.*, 1961; HOCHACHKA and SINCLAIR, 1962; WENDT, 1964 c). In this study the fish were fed heavily on a diet rich in carbohydrates during the summer, and significantly higher liver and muscle glycogen levels appeared in August (Table V) than in February—March (Table IV) when, although fed, they seemed to be starving. One group, starved for 25 days in February—March, showed no decrease in glycogen reserves nor in the coefficient of condition (Table VI) compared with the fed group (Table IV).

Smolt transformation may likewise have an influence on liver glycogen. It has been suggested that a high thyroid activity during the process is responsible for a decrease in liver glycogen (FONTAINE and HATEY, 1953; HOAR, 1953).

Usually liver and muscle glycogen levels in fish are considered to be low in comparison with corresponding mammalian tissues, and the ratio of liver to muscle glycogen is thought to be about 30 : 1 to 50 : 1 in fish compared with 10 : 1 in mammals (BLACK *et al.*, 1960). In this study the concentrations in August fell within the range reported for mammals, and the ratio of liver to muscle glycogen was about 7 : 1 both in February—March and August. Moreover another group of fishes, starved for 6 and 21 days in August, had a ratio of about 7 : 1.

As most fishes here examined were females, it was not possible to study the influence of sex. All precocious males were excluded as in February—March they showed higher liver and muscle glycogen values than did immature males (Table III), which was in agreement with an assumption by BLACK *et al.* (1961) for mature trout.

Strenuous exercise in salmonoids is known to cause a rapid depletion in muscle glycogen (BLACK *et al.*, 1960, 1962). In this study large quantities were lost in August, but there still remained about 0.299 g ⁰/₀ at the point of exhaustion (Table V). In February—March, when the unexercised level was only one-third of that in August, the decrease seemed to be more pronounced. At exhaustion there remained only 0.045 g ⁰/₀ (Table IV). No significant replenishment occurred within 15 hours at any time. Restoration in unfed rainbow trout was not complete after 24 hours, but feeding during recovery caused a more rapid replacement of glycogen stores (BLACK *et al.*, 1960).

Exercise to the point of exhaustion did not seem to cause any significant changes in liver glycogen at 0.2°C or at 15°C, although there was a tendency to lower values at the cessation of exercise (Tables IV, V). In the literature the results vary. MILLER *et al.* (1959) found no decrease in liver glycogen in pellet-fed (CLARK's dry rations) rainbow trout compared with liver-fed trout, which showed a significant decline during exercise. DEAN and GOODNIGHT (1964) obtained varying results in 5 species of temperate-zone fish. In the present investigation the levels fluctuated during recovery (Fig. 1; 2). One source of variation might have been the pale livers that appeared both in winter and summer. It is not clear whether they were "high-glycogen" livers or "fatty" livers. A weak replacement of depleted muscle glycogen and no feeding might have caused a slight decline in liver glycogen during recovery.

It is a well-known fact that the rate of mammalian enzyme reactions is directly and markedly effected by changes in temperature. As BROWN (1960) and MACLEOD *et al.* (1963) found it evident that the EMBDEN-MEYERHOF pathway is the main metabolic path in fish as well as in mammals, one might expect temperature changes to alter lactate production in fish. Further, BLAZKA (1958) found that the end products of anaerobic metabolism in fish at low temperatures were CO_2 and lipids. EKBERG (1962) and HOCHACHKA and HAYES (1962) supposed that the pentose shunt may be active at lower temperatures.

In my studies lower blood lactate values appeared both in *Salvelinus fontinalis* (WENDT, 1964 a) and in *Salmo salar* L. (this study) following strenuous exercise in February—March at 5°C and 0.2°C than appeared in August at 15°C (Fig. 1; 2). The unexercised levels obtained at 0.2°C (Tab. IV) are among the lowest ever published for fish. At both times the blood lactate continued to rise during the first part of recovery. After 2 hours the average level in August was 3 times that in February—March, but on both occasions it was 12 times the unexercised level. The higher summer values were in agreement with findings for other salmonoids at 11.5°C. (BLACK *et al.*, 1961) but BLACK (1957 a) found no difference in blood lactate between Kamloops trout (*Salmo gairdneri*) exercised by hand for 15 minutes at two acclimatization temperatures, 11.5°C and 20°C, nor did CAILLOUET, JR (1964) find any difference between mature carp at 1°C. (winter) and at 24°C. (summer). DEAN and GOODNIGHT recorded higher blood lactate values in *Micropterus salmonoides, Ichtalurus melas* and *Pomoxis anularis* after exercise at 5°C than at 20°C. In *Lepomis macrochirus* they found precisely the contrary, but the summer values were lower than those reported by HEATH and PRITCHARD (1962), who exercised *Lepomis* to fatique.

It is also known from the work of JOHNSON *et al.*, (1945) that lactate shows lower diffusion rates across the blood-cell membrane at lower temperatures, and a low rate of diffusion of lactate from muscle to blood has been considered to be at least partly responsible for the prolonged elevation of blood lactate in fish. In this study the disappearance of lactate from blood was slow at 0.2°C. After 15 hours of recovery the level was still about 5 times as high as the unexercised level (Table IV). At 15°C, however, the unexercised values were almost reached after 15 hours (Table V) in spite of a greater amount of lactate appearing in the blood during the first phase of recovery.

Thus it is not yet possible to describe the effect of exercise and temperature on the carbohydrate metabolism in fish. The physiological state seems to play a very important role. PARKER and BLACK (1959) proposed that cessation of feeding in connection with approaching maturity and entrance into fresh water is a contributing factor in the ability of Pacific salmon to migrate long distances upstream. The quickly available energy from liver and muscle glycogen is no longer obtainable, and the source of energy may be stored fat and "non-essential" protein which is presumably not quickly available. Thus the rate of energy supply may restrict the action of the fish and reduce struggling when it is stimulated. The same is thought to be the case in fed fish when these are starved for various periods before exercise. Some results in my investigations on immature *Salmo salar* L. are consistent with this hypothesis. One group fed on a raw diet in February—March was fatigued after an average time of 19 minutes, and another fed on pellets after 30.5 minutes. The difference was significant at $P=0.01$ level. The former had their stomachs filled with food all the winter, and they showed higher liver and muscle glycogen levels than did the pellet-fed salmon. These seemed to be starving. Their stomachs with few exceptions were empty, and the decrease in liver and muscle glycogen from November to February was great. In spite of 30.5 minutes exercise they showed only a tendency to a decrease in muscle glycogen, in contrast to the highly significant decline ($P < 0.001$) in the group fed on the raw diet which was fatigued after 19 minutes (WENDT, 1964 c). There also seemed to be a difference in behaviour during exercise. The raw diet-fed fishes struggled more violently and soon lost their headway when exercised, in contrast to the pellet-fed ones, which swam at a steady rate at the bottom of the swimming chamber until exhausted. The pellet-fed fish used in February—March in this study were fatigued after an average time of 32 minutes (p. 8). They showed, after being starved for 25 days, no decrease in liver or muscle glycogen or any difference in exercising time when compared with the fed group (Table IV; VI). In another group, acclimatized from 0.2°C to 11.5°C without feeding, only 3 out of 8 were fatigued within 60 minutes. In summer at 15°C (Table V) the pellet-fed fish were fatigued after an average time of only 21 minutes (p. 9). The difference in behaviour described above between pellet-fed and raw diet-fed fish was also seen between "winter" and "summer" animals fed on pellets.

Summary

1. The average coefficient of condition was in winter 1.143 and in summer 1.234.
2. The average unexercised liver and muscle glycogen levels were in winter 1.40 ± 1.37 g % and 0.190 ± 0.089 g %, and in summer 3.85 ± 1.11 g % and 0.593 ± 0.148 g % respectively. The ratio of liver to muscle glycogen was about 7 : 1 at both times.
3. Starvation for 25 days in February—March caused no decline in liver or muscle glycogen. In August liver glycogen decreased from an average of 3.85 ± 1.11 g % to 0.67 ± 0.37 g %, and muscle glycogen from an average of 0.593 ± 0.148 g % to 0.089 ± 0.026 g % after 21 days of starvation.
4. In winter, exercise to the point of exhaustion caused a decrease in muscle glycogen with 70 % to an average level of 0.045 ± 0.047 g %. In summer, the loss was 50 % to 0.299 ± 0.122 g %. Liver glycogen did not seem to be influenced by exercise.
5. During 15 hours of recovery there was a tendency to a replenishment of muscle glycogen at both times, whereas liver glycogen fluctuated.
6. After exercise to exhaustion the average blood-lactate level was 38.8 ± 13.3 mg % in winter against 76.3 ± 9.9 mg % in summer. Recovery caused a further rise to 57.1 ± 18.3 mg % and 175.4 ± 35.0 mg % respectively after 2 hours. Fatigue occurred in winter after an average time of 32 ± 8.1 minutes, and in summer after 21 ± 5.2 minutes.
7. In winter, after 15 hours of recovery the average blood lactate was 5 times as high as the unexercised level, 18.3 mg % and 3.3 mg % respectively. In summer, the corresponding average values were 21 mg % and 14.6 mg %.

Acknowledgements

I wish to express my gratitude to Professor RAGNAR FÄNGE, Head of the Institute of Zoophysiology, Gothenburg, and Dr. BÖRJE CARLIN, Director of the Salmon Research Institute. Dr. LARS-ERIK SUNDELL helped me in many ways and his never-failing interest and encouragement were most valuable. I am also greatly indebted to the staff of the Salmon Research Laboratory, Älvkarleö for their helpfulness and courtesy. For valuable technical assistance I thank Mrs. ELIZABETH JANSON and Mr. CURT ERIKSSON.

The studies were financially supported by grants from the Science Faculty of the University of Gothenburg and The Royal Fishery Board of Sweden.

Literature cited

Black, E. C. 1955. Blood levels of hemoglobin and lactic acid in some freshwater fishes following exercise. *J. Fish. Res. Bd. Canada, 12: 917—929.*

— 1957 a. Alternations in the blood level of lactic acid in certain salmonoid fishes following muscular activity. I. Kamloops trout, *Salmo gairdneri. J. Fish. Res. Bd. Canada, 14: 117—134.*

— 1957 b. Alternations in the blood level of lactic acid in certain salmonoid fishes following muscular activity. II. Lake trout, *Salvelinus namaycush. Ibid., 14: 645—649.*

— 1957 c. Alternations in the blood level of lactic acid in certain salmonoid fishes following muscular activity. III. Sockeye salmon, *Oncorhyncus nerka. Ibid., 14: 807—814.*

— Wing-Gay Chiu, F. D. Forbes, and A. Hanslip. 1959. Changes in pH, carbonate and lactate of the blood of yearling Kamloops trout, *Salmo gairdneri,* during and following severe muscular activity. *J. Fish. Res. Bd. Canada, 16: 391—402.*

— A. C. Robertson, A. R. Hanslip, and Wing-Gay Chiu. 1960. Alternations in glycogen, glucose and lactate in rainbow and Kamloops trout. *J. Fish. Res. Bd. Canada, 17: 487—500.*

— A. C. Robertson, and R. R. Parker. 1961. Some aspects of carbohydrate metabolism in fish. Page 89—124 in Comparative Physiology of Carbohydrate Metabolism in Heterothermic animals. Ed. A. W. Martin, Univ. Wash. Press 168 pp.

— Anne Robertson Connor, Kwok-Cheung Lam, and Wing-Gay Chiu. 1962. Changes in glycogen, puruvate and lactate in rainbow trout (*Salmo gairdneri*) during and following muscular activity. *J. Fish. Res. Bd. Canada, 19: 409—436.*

Blazka, P. 1958. The aerobic metabolism of fish. *Physiol. Zoöl.,* 31: 117—128.

Brown, M. E. 1957. Experimental studies on growth. In Volume I of The Physiology of Fishes. Ed. M. E. Martin, Univ. Wash. Press. 168 pp.

Brown, W. D. 1960. Glucose metabolism in carp. *J. Cell. Comp. Physiol., 55: 81—85.*

von Buddenbrock, W. 1938. Beobachtungen über das Sterben gefangener Seefische und über den Milchsäuregehalt des Fischblutes. *Cons. Inter. Explor. Mer. Rapp. et Proc. Verb. 101: 3—7.*

Buttkus, H. 1963. Red and white muscle of fish in relation to rigor mortis. *J. Fish. Res. Bd. Canada, 20: 45—58.*

Caillouet, Jr., Charles W. 1964. Blood lactic acid concentration of unexercised and exercised mature carp in winter and summer. *Iowa State J. Sci., 38: 309—322.*

Carlin, B. 1963. The Salmon Research Institute and salmon conservation in Sweden. The Salmon Research Laboratory at Älvkarleö. *Sv. Vattenkraftfören. Publ. Nr 502, pp. 223—259.*

Dean, J. M. and C. J. Goodnight. 1964. A comparative study of carbohydrate metabolism in fish as affected by temperature and exercise. *Physiol. Zoöl., 37: 280—299.*

Ekberg, D. R. 1962. Anaerobic and aerobic metabolism in gills of Crucian carp adapted to high and low temperatures. *Comp. Biochem. and Physiol., 5: 123—129.*

Fontaine, M. and J. Hatey. 1953. Contribution a l'étude du métabolisme glucidique du saumon (*Salmo salar* L.) à diverses étapes de son dévelopment et de ses migrations. *Physiol. Comparata et Oecol., 3: 37—52.*

Heath, A. G. and A. W. Pritchard. 1962. Changes in the metabolic rate and blood lactic acid of bluegill sunfish, *Lepomis macrochirus,* Raf. following severe muscular activity. *Physiol. Zoöl., 35: 323—329.*

Hoar, W. S. 1953. Control and timing of fish migration. *Biol. Rev., 28: 437—452.*

Hochachka, P. W. and F. R. Hayes. 1962. The effect of temperature acclimation on pathways of glucose metabolism in the trout. *Can. J. Zool., 40: 261—270.*

Hochachka, P. W. and A. C. Sinclair. 1962. Glycogen stores in trout tissues before and after stream planting. *J. Fish. Res. Bd. Canada, 19: 127—136.*

JOHNSON, R. E., H. T. EDWARDS, D. B. DILL, and J. W. WILSON. 1945. Blood as a physicochemical system. XIII. The distribution of lactate. *J. Biol. Chem., 157: 461—473.*

LAGLER, K. F. 1959. Freshwater Fishery Biology. Sec. Ed. WM. C. Brown Company, Dubuque, Iowa. 421 p.

LEIVESTAD, H., H. ANDERSEN, and P. F. SCHOLANDER. 1957. Physiological response to air exposure in codfish. *Science, 126: 505.*

MACLEOD, ROBERT A., R. E. E. JONAS, and E. ROBERTS. 1963. Glycolytic enzymes in the tissues of a salmonoid fish (*Salmo gairdnerii gairdnerii*). *Can. J. Biochem. Physiol., 41: 1971—1981.*

MILLER, R. B. 1958. The role of competition in the mortality of hatchery trout. *J. Fish. Res. Bd. Canada, 15: 27—45.*

— A. C. SINCLAIR, and P. W. HOCHACHKA. 1959. Diet, glycogen reserves and resistance to fatigue in hatchery rainbow trout. *J. Fish. Res. Bd. Canada, 16: 321—328.*

MILLER, the late RICHARD B. and F. MILLER. 1962. Diet, glycogen reserves and resistance to fatigue in hatchery rainbow trout. Part II. *J. Fish. Res. Bd. Canada. 19: 365—375.*

MONTGOMERY, R. 1957. Determination of glycogen. *Arch. Bioch. Biophys., 67: 378—386.*

NAKATANI, ROY. 1957. Changes in inorganic phosphate and lactate levels in blood plasma and muscle tissue of adult steelhead trout after strenuous swimming. *Tech. Rept. No 30, School of Fisheries, Univ. of Washington, Seattle.*

PARKER, R. R. and E. C. BLACK. 1959. Muscular fatigue and mortality in trollcaught chinook salmon (*Oncorhyncus Tschwytscha*). *J. Fish. Res. Bd. Canada, 16: 95—106.*

PARKER, R. R., E. C. BLACK, and P. A. LARKIN. 1959. Fatigue and mortality in trollcaught Pacific Salmon (*Oncorhyncus*). *J. Res. Bd. Canada, 16: 429—448.*

ROE, J. H., J. M. BAILY, R. R. GRAY, and J. N. ROBINSON. 1961. Complete removal of glycogen from tissues by extraction with cold trichloroacetic acid solution. *J. Biol. Chem., 236: 1244—1246.*

SCHOLANDER, P. F. and EBBA BRADSTREET. 1962. Microdetermination of lactic acid in blood and tissues. *J. Lab. Clin. Med., 60: 164—166.*

SECONDAT, M. et D. DIAZ. 1942. Recherches sur la lactacidémie chez le poisson d'eau douce. *Comp. Rend. Acad. Sci., 215: 71—73.*

WENDT, C. 1964 a. Blodlaktat, muskel- och leverglykogen hos 2-somrig till 2-årig lax (*Salmo salar* L.) före och efter ansträngning. *Laxforskningsinst.* (*The Salmon Research Institute*) *medd. 1964, 1, bil. 3.* (*English summary.*)

— 1964 b. Influence of low temperature on the blood lactate level in *Salvelinus fontinalis* after exercise. *Rep. Inst. Freshw. Res. Drottningholm, 45: 206—210.*

— 1964 c. Diet and glycogen reserves in hatchery reared Atlantic salmon during different seasons. I. Winter. *Int. Council Explor. Sea. C. M. 1964, No. 40. 8 p.*

Ecological notes on *Acanthobdella peledina* GRUBE found on grayling and brown trout

By EVERT ANDERSSON

Institute of Limnology, Uppsala, Sweden

Contents

I. Introduction

In the summer of 1963 I began an investigation of the feeding habits of the grayling (*Thymallus thymallus* L.) and brown trout (*Salmo trutta* L.) in an area of the upper branch of the Pite River, noted for its abundance in fish. I had made an orientation visit the previous year and noticed at that time that large numbers of the grayling and brown trout were infested with *Acanthobdella peledina* GRUBE. Along with other observations on the fish caught, some notes were taken on the occurrence of *Acanthobdella* and some samples were taken. The number of *Acanthobdella* per fish has been noted since 18 July 1963 and during the summer 1964 their position, size, and color variations were also noted. More than 550 fish were examined during the two summers.

Acanthobdella occurs as a parasite on Salmonids and has been found among others on grayling, brown trout, char, and whitefish (DAHM 1962). It occupies an interesting position midway between the earthworm and the leech. It has four pair of chaetae on each of the five front segments in the front part of the body and a sucker on the extreme back end. This distinguishes it from the true leeches and enables *Acanthobdella* to be attached with its body perpendicular to the fish body. Its distinctive characteristics have caused many descriptions to be made of *Acanthobdella*'s anatomy (ex. LIVANOW 1906). Of its biology we know, unfortunately, much less. Earlier Swedish studies which should be mentioned are LÖNNBERG 1936 and DAHM 1962.

Acanthobdella occurs in the northern parts of Europe and Asia, and in Sweden it has been found in Lapland (from the Pite River north), Jämtland (only one occurrence, from the Fax River) and northern Dalarna (DAHM 1962).

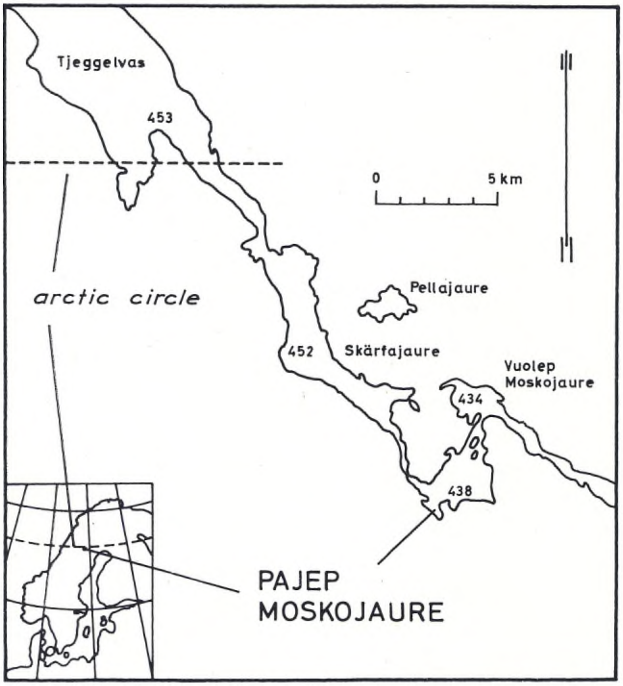


Fig. 1. Map of the area of investigation on the Pite River. The figures within the lake boundaries give the altitudes.

II. Description of the Area

Pajep Moskojaure is one of many lakes in the Pite River's upper course. It lies 40 kms north of Arjeplog and is surrounded by a forest consisting predominately of fir. The lake has an area of 5 km^2, its altitude is 438 m, and its greatest measured depth is 21.5 m. Both upstream and downstream is a chain of shorter stretches of stream alternating with other lakes. Fig. 1. The bodies of water named are nutrientpoor, and virtually uninfluenced by Man, since they are without dams and only a few families inhabit the area.

The greater part of Pajep Moskojaure has a sparse bottom vegetation. Near the shore the bottom is normally composed of sand and stone. As the depth increases, the mud layer becomes thicker. In the southern part of the lake the bottom slopes steeply as a rule. In the other parts it inclines slowly towards the middle of the lake, where the current has scoured a deep trench, which describes a bow between influx and efflux. Great quantities of water pass through the lake, and a rough estimate is that, in the summer, the lake's replenishment time is less than a week. This fact and the water's low temperature mean that no temperature stratification could be found. Temperature measurements during the summer 1964 showed a rise from 8.9°C (28 June) to 12.1°C (24 July), after which the temperature slowly sank. The Secchi disc depth increased from 12.7 m on 5 July to 14.0 m on 7 August. Values from 1962 (8 August) gave a pH of 7.0 and a specific conductivity (20°C) of $22 \cdot 10^{-6}$. The last two samples were taken at the outlet of the lake.

III. Methods

The grayling and brown trout for the investigation were caught with a net, a fly-rod, and a spinning-rod. Half of the graylings caught in the lake itself were netted. Most of the samples caught with the fly- and spinning-rods were kindly placed at my disposal by the members of the Heikkaklubb,[1] which leases the bodies of water in question. The fly and spin-caught grayling show the same tendencies in regard to the *Acanthobdella,* as those netted, so this former group can be considered a representative sample.

The fish were weighed when fresh and wet. An Ohaus scale with accuracy of 0.1 g was used, but here the weight is given in whole grams, as such a high degree of accuracy was deemed unnecessary. The length of the fish was measured from the nose to the end of the tail while the mouth of the fish was held closed and both lobes of the tailfin were folded together. Fish scales for the determination of age were taken on the left side of the fish, above the lateral line and below the posterior part of the dorsal fin. All the *Acanthobdella* material was preserved in a 4 ⁰/₀ formation solution, and therefore, all the given weights of *Acanthobdella* are based on preserved material. A Sartorius scale, with accuracy to 0.1 mg, was used. The preserving fluid was dried off, after which the animal was turned around on a piece of filter paper for one minute and then weighed. The sample was returned to the preserving fluid, where it lay for about one hour, and then a new drying and weighing was done. If the difference between the two weighings was greater than 0.2 mg, new weighings were made until the difference was equal to or smaller than that value. The mean of the two values was then taken, so that the deviation was ±0.1 mg.

For the determination of age, which was carried out only on the grayling, a plastic impression of the scales was obtained by pressing them between two plastic disc, with thickness of 0.5 and 1 mm. The thicker disc then served as a support, and on the thinner an impression of the scale was secured. This latter was placed in an enlarging apparatus, which magnified it 38 times, resulting in a clear picture of the scale. (This method agrees with that used at the Freshwater Laboratory in Drottningholm). As there exists a known relationship between scale size and fish length, and as each completed growth period is clearly marked on the scales, the length of the fish at different ages can be obtained by measuring the distance from the center to the indication of each growth period.

As the area under investigation showed different biotopes, it was divided into three sections. Section 1 embraced the stretch of stream between Pajep Moskojaure and Abmofallet, lying 1200 m upstream from the lake. The lake itself, exclusive of the outlet, comprised Section 2, and Section 3 was the outlet (Figs. 3 and 4).

---

[1] I should here like to express my sincere gratitude for the generous support given me by the Heikkaklubb.

IV. Results and Discussion

The *Acanthobdella* is found as a parasite on its host Salmonids only during a part of the year. LÖNNBERG (1936) writes, "They are apparently absent during the spring and until approximately the end of June. Probably they begin to appear during the first half of July. Then they persist well into late fall". Earlier published reports show that *Acanthobdella* has been found as early as 2 July to 8 July, and as late as 11 Oktober (DAHM 1962). These dates for the parasite attack agree with my observations. In 1963 the first find was on 2 July while in 1964 the first find was on 26 June and the second on 30 June. It should be noted that each year's first find was made on the opening day of the season, so that it is likely that one could find *Acanthobdella* even earlier.

Figure 2 shows the percentage of infested fish during different periods of the summer. The material has been divided into 5-day periods beginning on 26 June. As seen from the figure, there is less infestation on the brown trout during the first three 5-day periods (9 ⁰/₀) than later (34 ⁰/₀). These early periods have been omitted in the following discussion, as they may be considered as the time when the parasite attacks the fish. Moreover, 91 ⁰/₀ of the brown trout were taken in Section 1 and the rest in Section 2, while the outlet (Section 3) is not represented for this period.

In the three sections of the area under investigation, there occur differences in the percentage of infested fish and the number of leeches per fish. Figures 3 and 4 illustrate these differences. The abscissa gives the number of *Acanthobdella* per fish, the ordinate the number of infested fish, and the dark-colored circle section represents the per cent of fish infested. The number under the circle gives the number of fish investigated, and within parentheses is given the mean number of *Acanthobdella* per infested fish. As we see from Figure 3, in 1964 the lowest per cent (29) of infested grayling is found in the lake itself where the water is calmest. Throughout the upstream section, where there is flowing water, the frequency is 41 ⁰/₀; at the outlet it is 47 ⁰/₀. According to the inhabitants of the area, the parasite has "always" been abundant at the outlet. A similar picture was obtained in 1963 with the exception of a higher per cent for the fish in the lake, which may have been due to the scanty data. The total for the whole area indicates that the intensity of infestation is similar for the two years. For 1963 the value is 37 ⁰/₀ and for 1964 39 ⁰/₀. The picture is quite different for the brown trout. During both years the parasite appears most commonly on the fish in the lake itself. Moreover, *Acanthobdella* is much commoner during 1964 (34 ⁰/₀) than 1963 (15 ⁰/₀) (Fig. 4).

There is a wide variation in the number of *Acanthobdella* per fish (Fig. 3 and 4). Maximum values from three successive years are 60 specimens on the dorsal fin of a grayling (29 July 1962), 103 on a brown trout (20 July 1963), and 55 from a grayling (22 July 1964). A more detailed inspection of

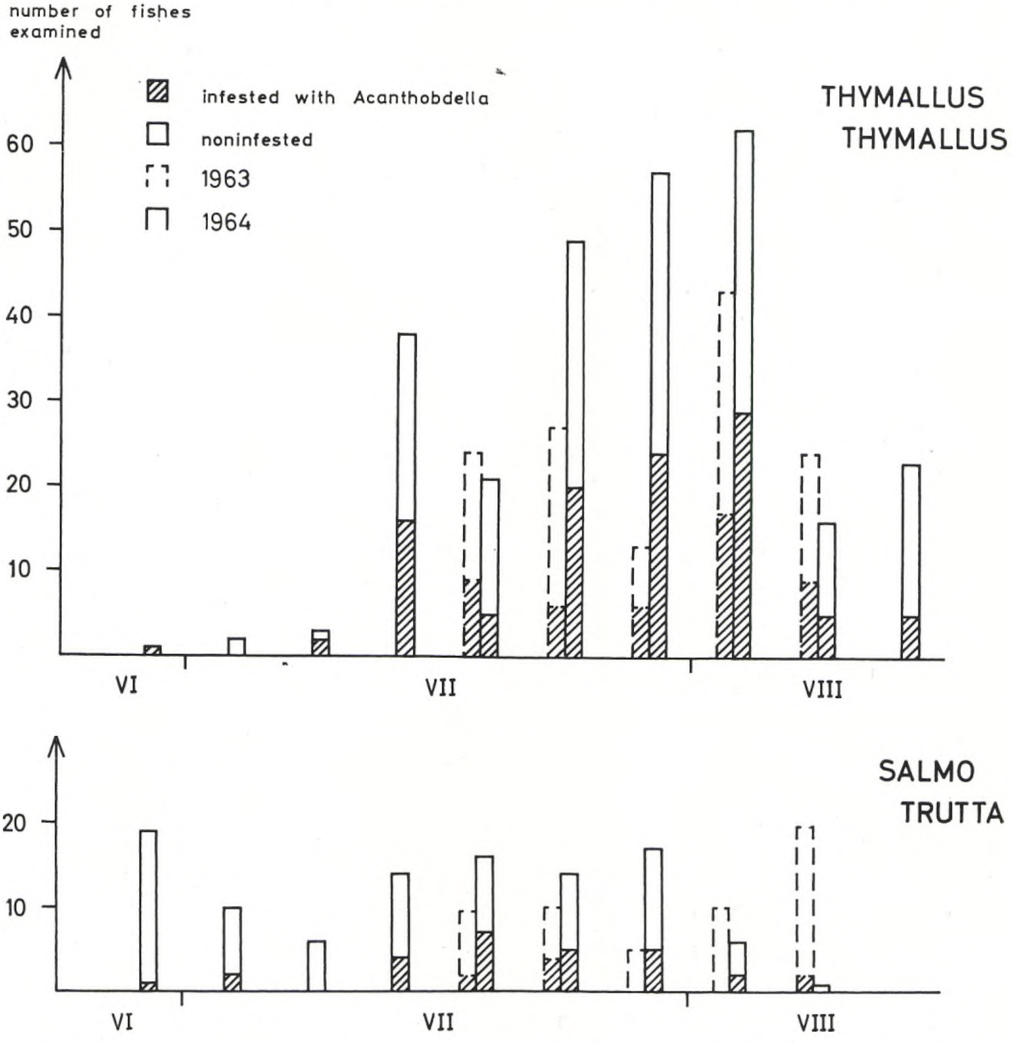


Fig. 2. The number of infested fish at different periods during 1963 and 1964. Each bar represents one 5-day period, beginning 26 June.

the data on the 104 *Acanthobdella*-infested grayling from 1964 reveals that 45 (43 %) have one, 34 (33 %) have 2—5, 18 (17 %) have 6—20 and 7 (7 %) more than 20 *Acanthobdella*. A similar frequency distribution is found on the other fish. For the number of *Acanthobdella* per fish in the different sections, the picture is totally different. In 1964 Section 1 has 5.6 *Acanthobdella* per infested grayling, while the corresponding value for the lake is 4.1 and for the outlet only 2.5 (Fig. 3). (So that a single extreme value should not unbalance the proportions within the sections, the highest value in each section has been omitted.) The average for the whole area is 4.4.

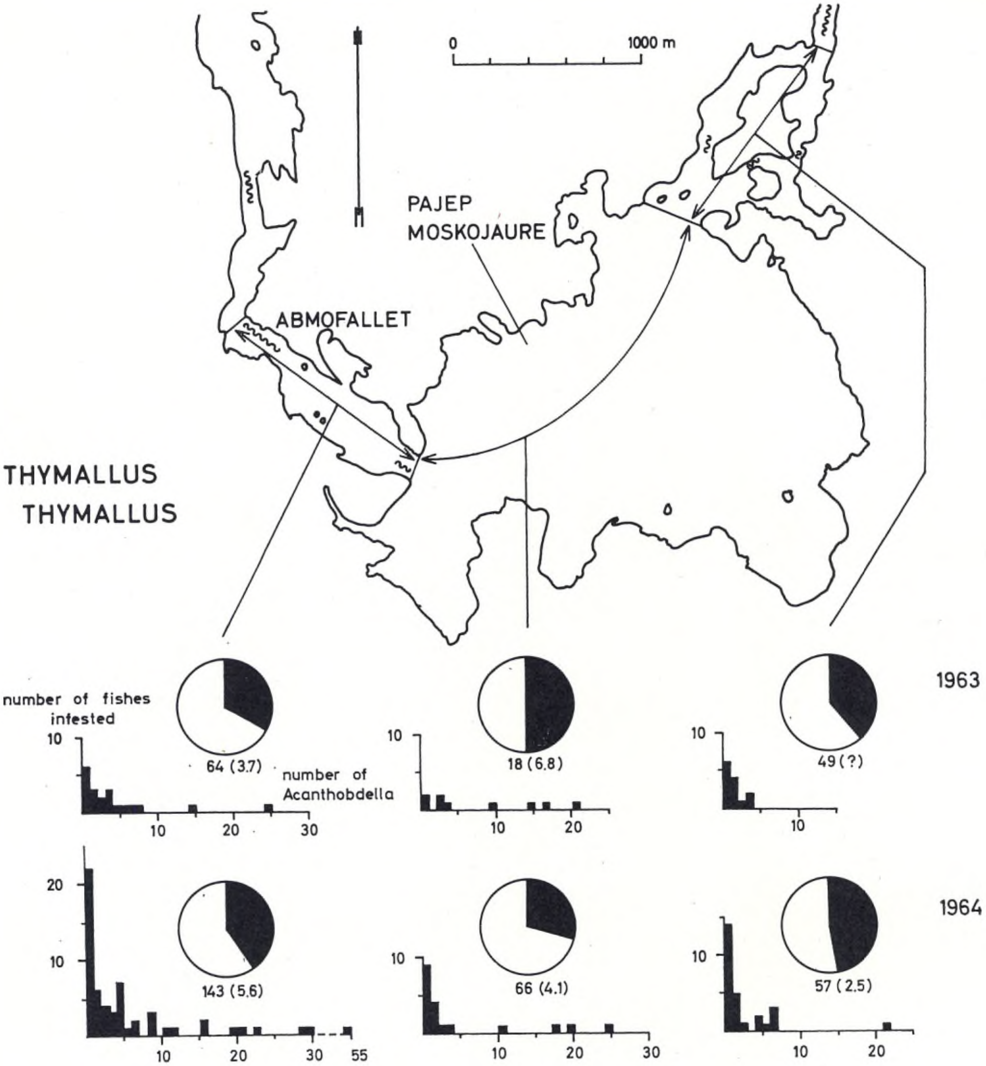


Fig. 3. Comparison of *Acanthobdella*'s occurrence on the grayling (*Thymallus thymallus*) in the different sections of the lake, 1963 and 1964.

◔ = fish infested by *Acanthobdella*
○ = fish not infested by *Acanthobdella*
∿ = current
n = number of fish examined
(m) = mean number of *Acanthobdella* per infested fish

The brown trout's highest value is found in the lake for both 1963 and 1964; the mean value for the latter year is 3.1 *Acanthobdella* per infested fish (Fig. 4).

The biology of the *Acanthobdella* and the fish must be kept in mind when looking for the cause of these variations. DAHM (1962) states that the *Acan-*

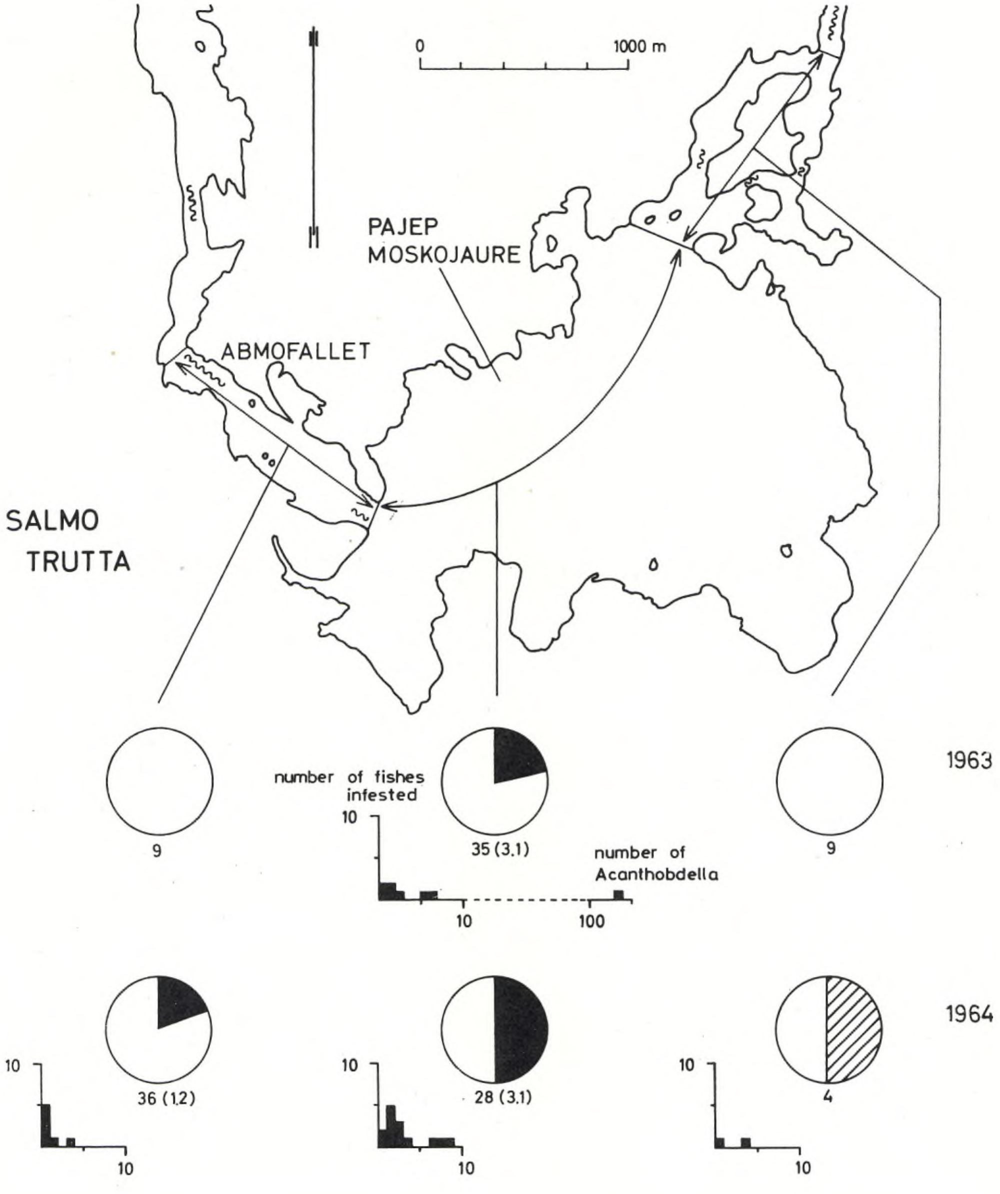


Fig. 4. Comparison of *Acanthobdella*'s occurrence on the brown trout (*Salmo trutta*) in the different sections of the lake, 1963 and 1964.

◔=fish infested by *Acanthobdella*
○=fish not infested by *Acanthobdella*
〰=current

n=number of fish examined
(m)=mean number of *Acanthobdella* per infested fish

thobdella, ethologically speaking, is similar to other fish leeches (e.g. *Piscicola geometra*), which lie attached to the bottom vegetation, waiting for the opportunity to attack a fish. To support this assertion, he notes that *Acanthobdella* occurs less often in those parts of the Lule River which are regulated, and in which, therefore, the bottom vegetation is reduced or absent. Concerning the biology of the fish, there occur differences between the various species, within different sizes of the same species, etc. This means that the different groups have different opportunities for coming in contact with *Acanthobdella*. Territorial behavior, choice of food, and choice of locale are all influencing factors. Different mating times can also be important in this connection.

There is also a variation in infestation related to the size of the host fish. These have been divided into size groupings, 15.0—19.9 cm, 20.0—24.9 cm, 25.0—29.9 cm, etc. Grayling less than 30 cm long are infested to a lesser degree than those of greater length, while grayling longer than 45 cm show a somewhat lower percentage of infestation than fish of medium size. The brown trout shows a similar trend, but the data is too limited for any definite conclusion (Fig. 5).

There is no difference in infestation between male and female fish. In 1964, 41 % of the female grayling and 33 % of the female brown trout are infested, while the corresponding values are 39 % for all grayling specimens and 34 % for all brown trout.

The position of *Acanthobdella* on the host fish is given in Figure 6. In that figure "f" means that the *Acanthobdella* appear only on that fin from which the arrow arises, "f+1" that the *Acanthobdella* appear on the indicated fin plus one additional fin, etc. The parasites generally lie on the dorsal fin. They are attached sometimes on the fin itself, sometimes at the base of the fin, usually on the back part (Fig. 7). 88 % of the grayling specimens from 1964 have *Acanthobdella* on the dorsal fin itself and at the fin's base, and 69 % have the parasite only on the dorsal fin. On the remaining grayling the parasites are nearly evenly distributed on the other fins. Thus, there exists a clear preference for the dorsal fin as the attachment point. The brown trout presents a similar picture, but there we find, in addition, a few exemples of *Acanthobdella* fastened along the lateral line, even with the anal fin. The reason that *Acanthobdella* usually is found on the fins is that they can easily attach themselves there. According to LÖNNBERG, the parasites prefer the back part of the dorsal fin because there they are best protected from the stream current. Conflicting statements exist in earlier writings concerning this placement of *Acanthobdella* on the host fish. Writing on the brown trout, trout, and grayling, POPPIUS (1900) said that *Acanthobdella* lie most often on the "fish's pectoral and ventral fins, less often at the anal, tail, and dorsal fins". It is not stated how many fish were inspected as a basis for these observations. DAN ANDERSSON states (letter to LÖNNBERG 1936) that they lie

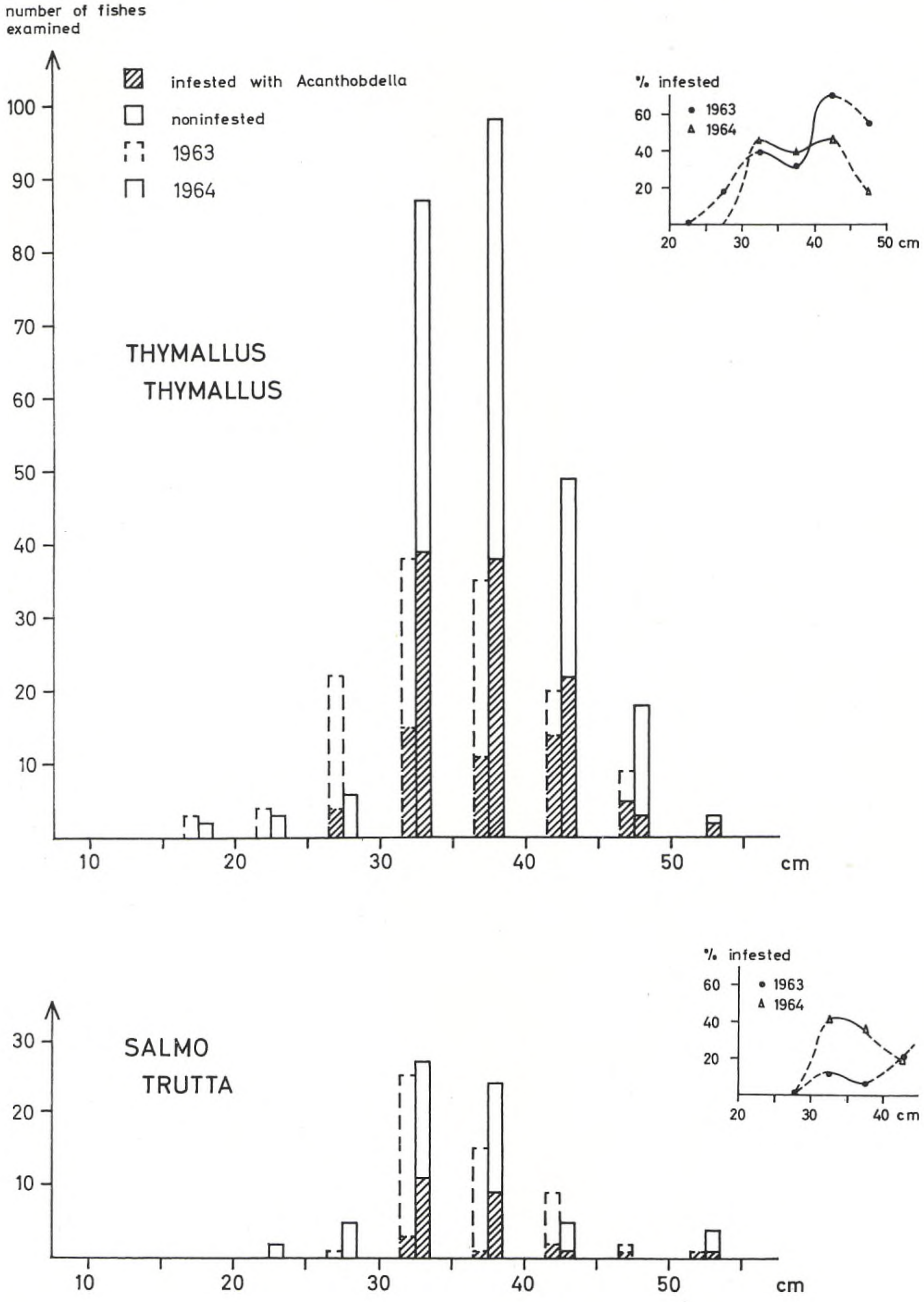


Fig. 5. The number of infested fish by size groupings. 15.0—19.9 cm, 20.0—24.9 cm, 25.0—29.9 cm, etc.

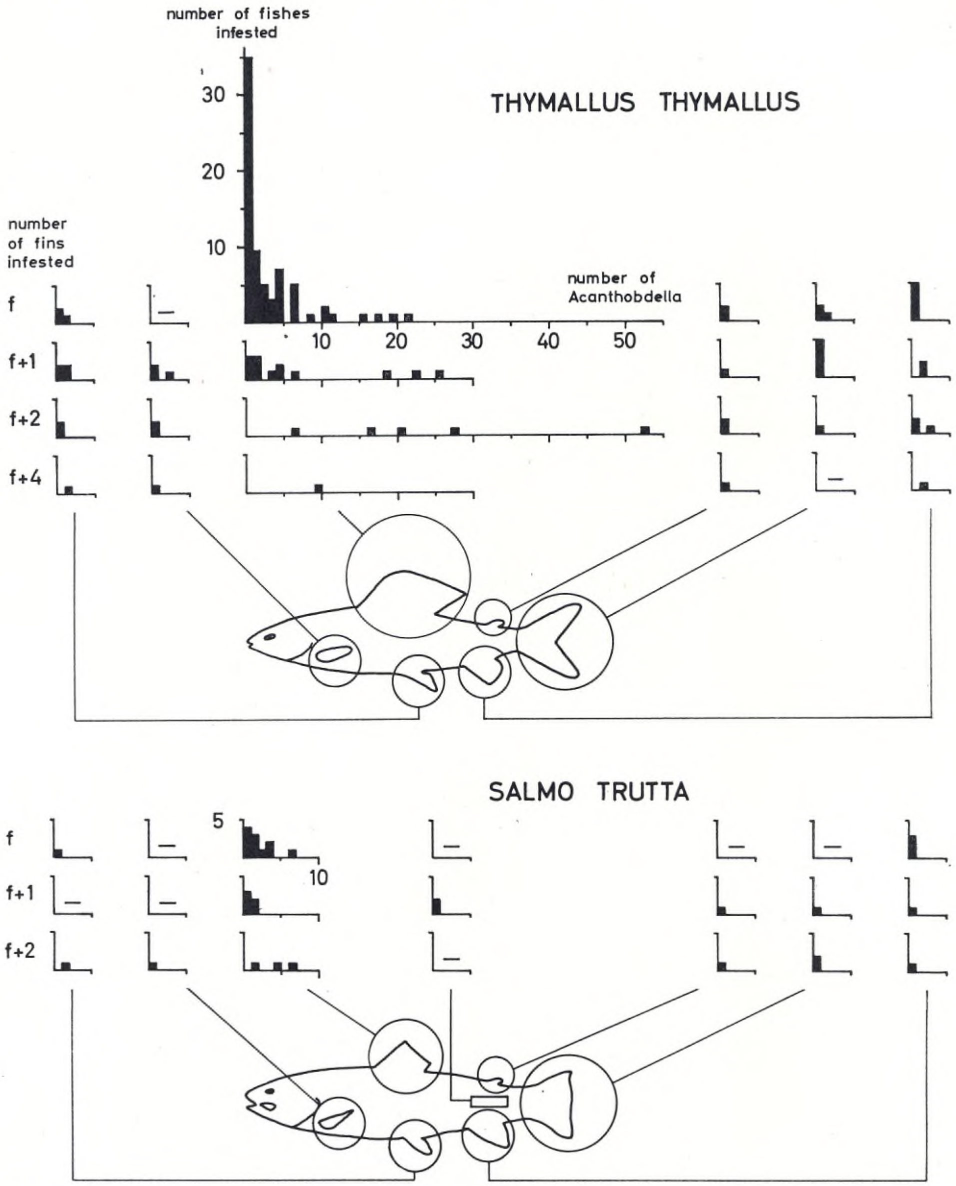


Fig. 6. Location of *Acanthodbella* on the host. f=*Acanthobdella* appears only on that fin from which the arrow arises, (f+1)=*Acanthobdella* appears on the indicated fin plus one additional fin, etc.

on the dorsal fin, adipose fin, ventral fin, and in a few isolated instances, on the anal fin. DAN ANDERSSON's observations were made in the Lule River and agree with my own.

As stated earlier, *Acanthobdella* appears during approximately four months

Fig. 7. *Acanthobdella* at the fin's base (above) and on the fin itself (below).

of the year as a parasite on Salmonids. DAHM (1962) writes, "Though there are no definite observations, it seems appropriate to infer that the specimens infest the fish in early summer, proceed through a period of growth and gradual sexual development which is eventually reached in the late autumn. After completing the sexual cycle, the individuals apparently die, as all samples from earlier in the year are comprised of small, sexually immature specimens". This supposition regarding the growth and development is supported by my own observations. At the beginning of July the *Acanthobdella* are normally about 1/2 cm long, but the size increases continually, and by the beginning of August they are a few cm long. In addition, *Acanthobdella*-free fishes have been found with a deformed dorsal fin as a result of an earlier infestation, presumably from some previous year. However, there are exceptions to this. As seen from Figure 8, a large specimen (125.4 mg) was found as early as 13 July 1964, and specimens in the 10 mg size range were found as late as 2 August 1964. In this connection, it should be emphasized that the material collected after 11 July 1964, and which is presented in Figure 8, was preserved because of some peculiarity, e.g., that the *Acanthobdella* were especially numerous or small, or that the color variation was notable. This material was therefore not used for the conclusions on the summer growth of *Acanthobdella*, even though one can see there the tendencies as discussed. Size distribution in the preserved material varies markedly throughout the same population. The largest sample is up to 7 times (mean value, 3.9) larger than the smallest (Fig. 8).

Color variation in *Acanthobdella* is marked. Usually they are grey-green to yellow-brown with dark crossbands. There are, however, successive gradations from this coloration to pure yellow without crossbands. The same individual can be dark in the middle and lighter towards the ends, etc. These yellow specimens appear during the entire investigation period (Fig. 7).

The question of the effect of *Acanthobdella* on the growth and condition of the fish is of great interest for fishery biology. To attempt to determine if the growth of the fish is influenced by *Acanthobdella*, growth studies were made on a number of grayling caught during the week of 28 July—3 August 1964. These fishes had then been infested by the parasite for about a month. Studies were made of the most abundant age-group, that is, the group of fish born in 1959 and which were in their sixth summer. Through growth line measurements on the fish scales, it was possible to determine their size before the 1964 growth period began, i.e., their size at 5 years. For 11 grayling, who completely lacked apparent ectoparasites, the average length was 31.6 cm, and for 9 specimens, which only had *Acanthobdella* as ectoparasites, the average length was 31.7 cm. From this 5-year-size to the end of July the growth was 2.3 and 2.4 cm, respectively, for the different groups. Even if the number of measured fish is very low, it can still be stated that no significant difference exists. It ought to be noted that, as the *Acanthobdella* are

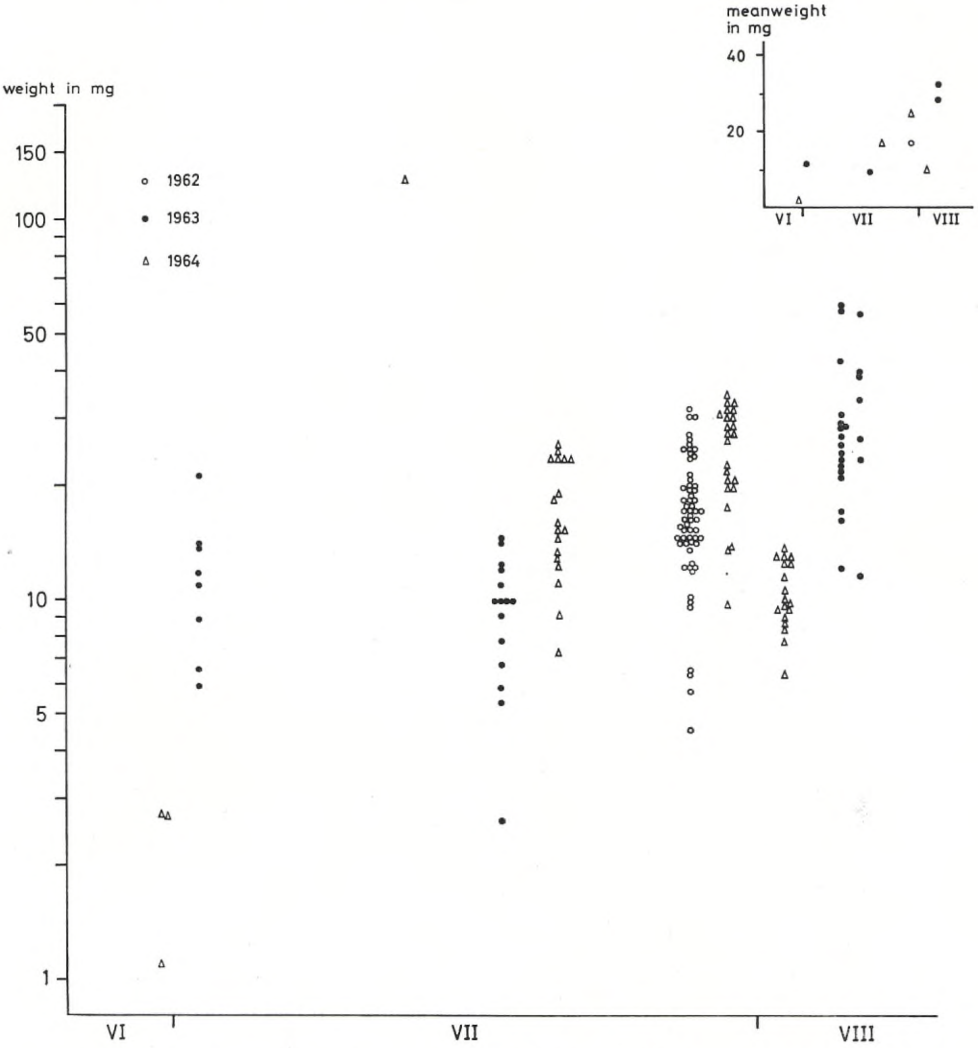


Fig. 8. Size distribution of several *Acanthobdella* populations from 1962—1964.

small at the beginning of the season, their effect during that period is less than later. To what degree the rate of growth is affected during the period from early August to October is a question which can not yet be answered.

Opinion seems to be divided as to whether *Acanthobdella* affects the general condition of the fish. POPPIUS (1900) writes that there were large sores around the fins and that when the *Acanthobdella* was numerous, the fish looked "rather thin and wretched". DAN ANDERSSON communicated to LÖNNBERG (1936) that "the fish does not appear to suffer visibly from being infested, and that there is no difference in flesh and liveliness between the infested fish and those few samples one catches which don't have parasites".

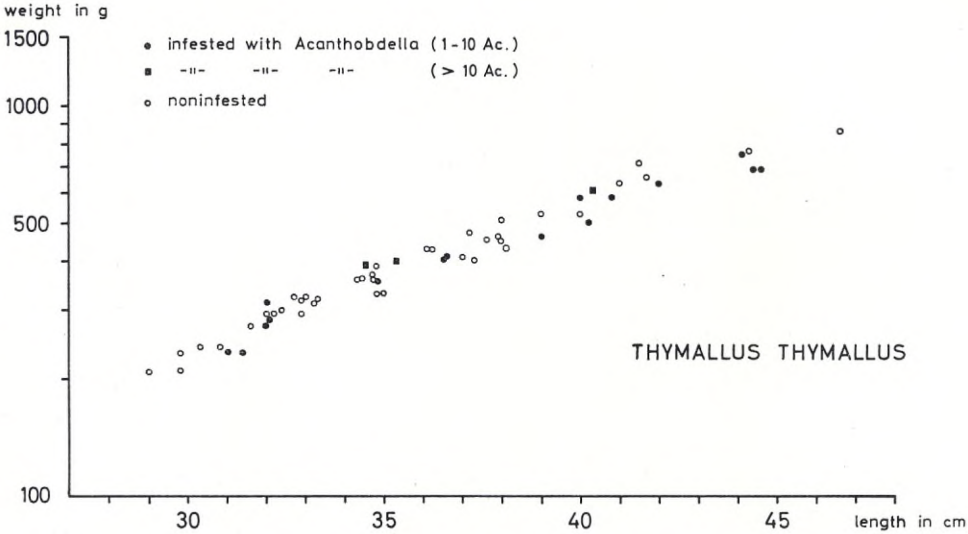


Fig. 9. Length and weight of grayling (*Thymallus thymallus*) with and without *Acanthobdella* from 30 July to 13 August.

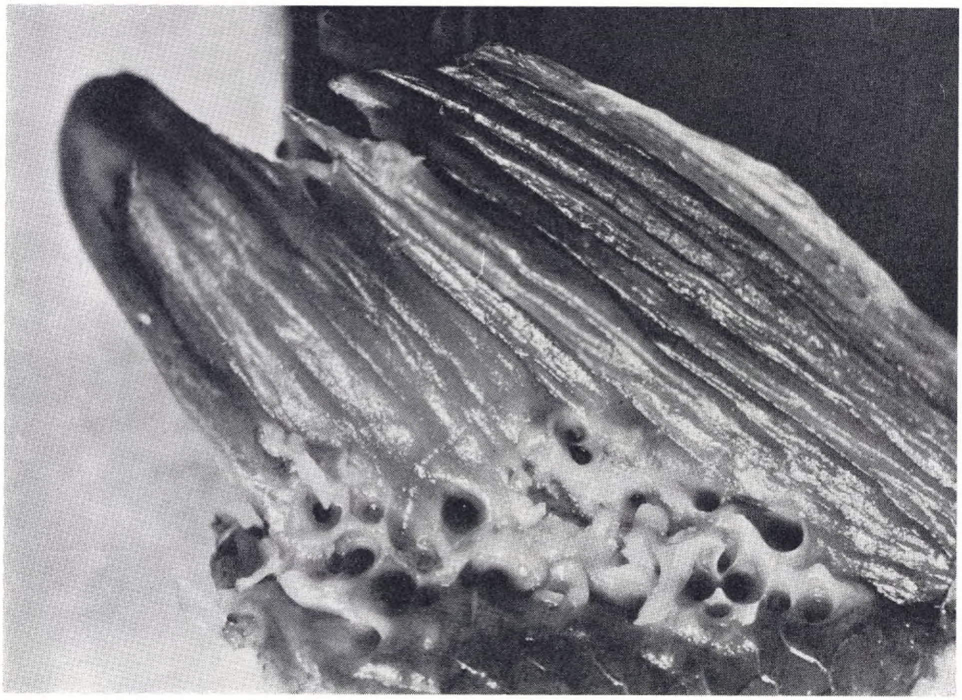


Fig. 10. Appearance of wound after the removal of *Acanthobdella* from the dorsal fin of the grayling (*Thymallus thymallus*). Cf. Fig. 7.

Unfortunately, data are also missing from the late fall period, when the fish have had the parasite for a longer time. Instead, grayling caught between 30 July and 13 August 1964 were used. Their weights and lengths have been used to make a length-weight diagram (Fig. 9). From this diagram we see that there is no difference between the infested and parasite-free fish. Not even those fish who have more than 10 *Acanthobdella* are apparently affected by the parasites. However, one may ask whether the *Acanthobdella's* parasitism affects the fish after a longer period. Even if the parasite does not visibly affect the host fish, the indirect effect must be considered. Every *Acanthobdella* causes a wound (Fig. 10), and these serve as easy entrances for fungi and bacteria. This risk of infection is not negligible, as is seen from examples of wounds on fish from other causes; during both summers fish were found which had been damaged by fish-eating birds, and in these cases the decaying process had advanced so far that the fish had a noticeable odor of decay.

V. Summary

During the investigations of the fishery biology and limnology of the Heikka area of the Pite River during the summers of 1963 and 1964 notes were taken on *Acanthobdella*'s occurrence on more than 550 fish. These data show that the organisms occur rarely at the end of June and the beginning of July, then become more common. The infestation affects smaller fish (< 30 cm) to a lesser degree than larger fish; no difference is found between the per cent of infested male and female fish. In the entire area under investigation 39 % of the grayling and 34 % of the brown trout were infested by *Acanthobdella* in 1964. Certain differences appear in the different sections of this area. The parasites are most often attached to the dorsal fin or to its base. They appear also on and at the base of other fins and in a few cases on the lateral line. The *Acanthobdella* showed continual growth during the period of investigation. Variations in both size and color exist within the same population. Normally *Acanthobdella* is grey-green to yellow-brown with dark crossbands, but yellow specimens exist. Those fish which were infested by *Acanthobdella* during their first month as parasites show the same rate of growth and condition as non-infested fish.

VI. References

DAHM, A. G. 1962. Distribution and biological patterns of *Acanthobdella peledina* GRUBE from Sweden (*Hirudinea acanthobdellae*). — *K. Fysiogr. Sällsk. Förhandl., 73: 10.*

LIVANOW, N. 1906. *Acanthobdella peledina* GRUBE, 1851. — *Zool. Jahrb. Jena (Anat.), 22.*

LÖNNBERG, E. 1936. Borstigeln, *Acanthobdella*, funnen i Sverige, en intressant nyhet i vår fauna. — *Fauna och Flora, Uppsala, 31.*

POPPIUS, R. 1900. Förekomsten af *Acanthobdella* i våra lappmarker. — *Medd. Soc. Fauna. Fl. Fenn., 24.*

Limnological studies in Hyttödammen

3. Zooplankton

By Rolf Arnemo

Institute of Limnology, Uppsala, Sweden

Contents

I. Introduction

In the first article of the series "Limnological studies in Hyttödammen" (Arnemo 1964) information was given about the pond and its physical and chemical conditions. In addition, earlier investigations of the pond were reviewed. The second article described the phytoplankton and the primary production of the pond (Arnemo and Nauwerck 1965). In this third article the qualitative and quantitative composition of zooplankton in Hyttödammen will be described with special regard to environmental factors.

The aim of the series of articles about Hyttödammen is to expand our knowledge of Swedish ponds used for the rearing of fish. Earlier investigations about zooplankton in Swedish fish ponds have been performed at Aneboda (Nordquist 1921) and at Bergeforsen (Grimås *et al.* 1954). These investigations yielded both qualitative and quantitative data. However, the quantitative data of NORDQUIST concerns only the total standing crop of plankton given as wet volume. In these investigations the sampling intervals were longer than in Hyttödammen, and so comparisons cannot be made.

There are also some published articles that deal only with the rotifers of the ponds at Aneboda. Through the works of LANG (1928), ALLGÉN (1933, 1935 a and b), CARLIN-NILSSON (1935) and BĒRZIŅŠ (1950, 1956) the rotifers are well known in this area.

As a rule I have chosen to compare the results obtained in Hyttödammen only with those obtained in investigations performed in about the same climate and using the same methods. Of these two are of special interest, namely that from the large Erken (NAUWERCK 1963) and that from the small Ösbysjön which approaches pond-like conditions (PEJLER 1961, 1962). As will be shown, Hyttödammen resembles a pond in some, though not in all details, and is therefore one stage in the lake-pond continuum.

An earlier article (ARNEMO 1960) gave the results, including zooplankton studies, of the first year of the investigation (1959). As will be shown, the present results, covering 1959—62, do not always agree with the earlier study. It is likely that the long-term study gives more significant results than the one year study.

II. Methods

1. Field methods

The sampling sites D and 1—4 are the same as those described by ARNEMO (1964, p. 12). At site 4 samples were taken at the surface, 1 m below, and at the bottom (2 m). Samples were also taken at some other sites, namely 1 a, A, B, E, 9 and 10 (Fig. 1), which have not been mentioned earlier. Site 1 a represents the water coming into Hyttödammen from the inlet pond, which receives the water from the river Dalälv via the flume (see ARNEMO 1964, p. 8 and Figs. 1 and 2). It was used from September 1961. The other new sites were used between October 28, 1960 and April 14, 1961 when the pond was not entirely filled with water. All the sites used before October 28, 1960, except site 4, were dry then and the depth at site 4 was only 1 m instead of 2 m. Sites A, B, and E represent water from springs. Site 9 represents water entering the pond through the main ditch. Site 10 represents the water in the pond just at the surface outflow of the pond.

Samples were taken at all these sites mainly to show the temporal succession of zooplankton, but some idea may also be gained of its spatial distribution. As a rule the frequency of sampling was once a week during summer but after about mid-September the sampling was irregular and less frequent. The sampling dates can be seen in the Figures showing the distribution of the species. From the beginning of the investigation the samples were taken

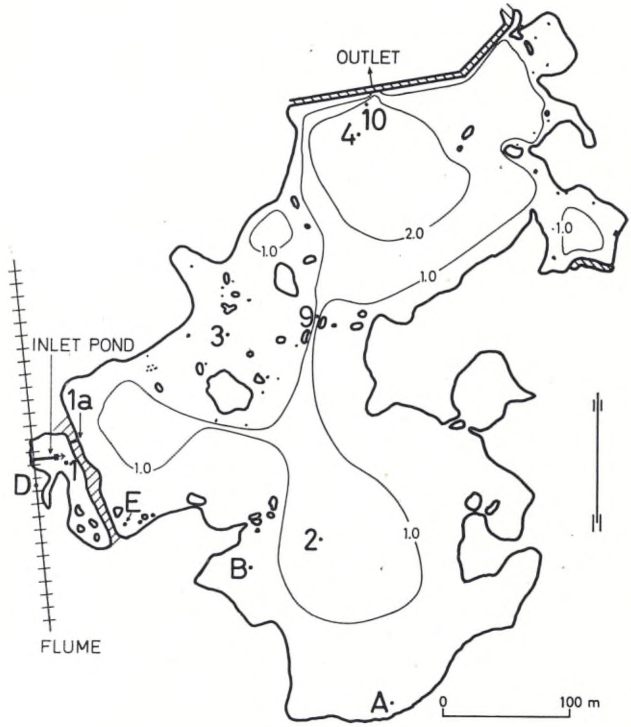


Fig. 1. Hyttödammen. Depth contours and sites (A, B, D, E, 1 a, 1—4, 9, 10).

with a Ruttner sampler, capacity 1.6 litres. From July 10, 1961 to September 4, 1961, samples were taken with a RUTTNER sampler and for comparison also with a plexiglass tube (see ARNEMO 1964, p. 13), capacity c. 6 litres. The results of the comparison of the methods are given on pp. 207—8. After September 10, 1961 samples were taken only with the plexiglass tube, except at site 4, where the vertical distribution was studied with a RUTTNER sampler as before. The plexiglass tube has been used in ponds by other authors (SCHÄPERCLAUS 1961, STRAŠKRABA 1963); it resembles the sampler described by WUNDER (1935). The 1 litre samples were fixed in the field with LUGOL's solution plus acetic acid (NAUWERCK 1963, p. 15).

To get a more detailed picture of the horizontal distribution, samples were taken (c. 30 sites) during the summers of 1961 and 1962 at approximately monthly intervals with the plexiglass tube.

For qualitative use, net samples were taken with a 80 μ mesh net (MÜLLER gauze No. 25) and fixed with formalin. They were taken once a week near the outlet, where the higher aquatic vegetation is more or less absent.

2. Laboratory methods

The zooplankton was concentrated by sedimentation of the 1-litre samples in tall cylinders and stored in bottles. Counting of the zooplankton was done with an inverted microscope and counting chambers.

The calculations of the volume of individuals of the most important species were made stereometrically (Axelson 1961, p. 139, Nauwerck 1963, p. 98—100). The values found for the Hyttödammen species agree generally with those found by the other authors for the same species. The species found in Hyttödammen had the following mean volumes given as mm^3. (Although the volumes of the *Rotatoria* have been determined, they are not included in the list because of their limited role.)

Cladocera:	*Limnosida frontosa*	0.08
	Diaphanosoma brachyurum	0.06
	Holopedium gibberum	0.15
	Daphnia cristata	0.1
	Scapholeberis mucronata	0.04
	Simocephalus vetulus	0.1
	Ceriodaphnia reticulata	0.05
	Bosmina coregoni+longirostris	0.06
	Ophryoxus gracilis	0.07
	Eurycercus lamellatus	0.3
	Camptocercus lilljeborgi	0.04
	Acroperus harpae	0.05
	Rhynchotalona rostrata	0.01
	Graptoleberis testudinaria	0.04
	Alonella	0.01
	Pleuroxus trigonellus	0.02
	Chydorus sphaericus	0.1
	Polyphemus pediculus	0.05
Copepoda:	*Nauplii* of *Calanoida*	0.001
	Copepodids I—III of *Eudiaptomus graciloides*	0.03
	Copepodids IV—V+adults of *Eudiaptomus graciloides*	0.07
	Copepodids I—III of *Heterocope appendiculata*	0.07
	Copepodids IV—V+adults of *Heterocope appendiculata*	0.45
	Nauplii of *Cyclopoida*	0.0005
	Copepodids I—III of *Cyclopoida*	0.01
	Copepodids IV—V+adults of *Cyclopoida*	0.05

3. Construction of diagrams

The diagrams illustrating results of the year-round temporal and spatial studies are of the same type as explained by ARNEMO (1964, pp. 15—18, the results from the physical and chemical investigation over time). The diagrams in the present article are slightly modified by having the different sampling sites separated from one another by lines. In spite of the well-known uneven distribution of organisms in lakes and ponds, isopletes have been drawn in the diagrams so as to show the differences in distribution between the sites and over time. The values for the isopletes were arbitrarily chosen to emphasize the differences.

In the diagrams illustrating the summer studies of horizontal distribution the values of the isopletes are chosen in the same manner as above. Even with the large number of stations the errors involved in drawing isopletes may be largely due to the patchiness of the zooplankton (e.g. NAUWERCK 1963, pp. 17—23). This is especially true in the areas close to the shore. Thus, the isopletes should be taken only as indications of possible differences between areas.

Usually, a dot in the Figures means that a sample was taken. If there is no number next to the dot, no animals of that particular species were found. However, when the horizontal distribution is plotted on a map, the point is difficult to see. In this case, a zero is always written if no individuals were found. A question mark means that the sample was lost. Where the value was derived from a calculation, a plus sign means that the value found was smaller than 0.01 mm^3/l or 1 $^0/_0$.

Special symbols are used in the temporal and spatial distribution diagrams to indicate modification of the zooplankton relationships by fish. The fish symbol means that newly-hatched fry were placed in the pond at the date indicated by the accompanying arrow. The numeral 1 at the arrow indicates sea-run trout (*Salmo trutta* L.) and the numeral 2 indicates salmon (*Salmo salar* L.). About 30,000 sea-run trout and 200,000 salmon are introduced yearly, but in November 1961, only 40,000 salmon were put in. The young fish prey on the zooplankton, but it is difficult to estimate their importance. By stomach analysis, it is possible to determine which species of the zooplankton are eaten by fish (a plus sign in the diagram). Although the stomach analyses will be dealt with in a later article, it may be noted here that the species and relative number of zooplankton eaten were the same for both species of fish. A plus sign in parentheses indicates that some of the zooplankton in the diagram are eaten by fish. If the balance of the total zooplankton community is influenced by predation, it is likely that the zooplankters which are not eaten will be indirectly affected; these species are therefore indicated by a fish without any other symbols.

4. Limitations

There are many factors that influence the qualitative and quantitative distribution of zooplankton. In this investigation it has not been possible to examine the effect of all of them. Thus the effect of predation by young fish upon zooplankton can only be surmised, owing to the difficulties of estimating this effect quantitatively. The literature about the relations between the standing crop of different food organisms and the growth and population densities of fish is extensive. NORDQUIST (1921) pointed out that investigators who calculate an expected yield of fish from the standing crop of bottom fauna and zooplankton must consider the effect of predation. The idea was also stressed by NAUMANN (1927) when he suggested a classification of ponds, and by WALTER (1934) in his handbook of fishery biology. Since then many authors have reported observations from lakes and ponds concerning the influence of predation upon the zooplankton and the bottom fauna (RICKER 1937, HAYNE and BALL 1956, LELLAK 1957, HRBÁČEK 1958, HRBÁČEK *et al.* 1961, JOHNSON 1961, GERKING 1962, GRYGIEREK 1962, STRAŠKRABA 1963 and LÖTMARKER 1964); but some authors have found no effect of predation at all (SCHÄPERCLAUS 1943 and BARTHELMES 1963). The divergences observed by these authors may possibly be explained by the different degree of utilization by different species of fish of either bottom fauna or zooplankton or both. Part of the difference lies in the different food-seeking habits of the fish. Another consideration is the population densities of predator and prey, and the reproduction rate of the prey. Several authors (IVLEV 1961, GRIMÅS 1963) have pointed out the difference in reproduction rate between the zooplankton and bottom fauna, and the difference in availability.

The *Protozoa* have not been taken into consideration in this investigation.

The list of *Rotatoria* is far from complete. Many of the forms are impossible to identify as to species when preserved. Special samples of the benthic forms have not been taken but those occurring in the samples have been determined and have been added in the calculations.

Other factors of importance to the distribution of the zooplankton are the occurrence of swarms (patchiness) and the diurnal migrations found in many species. Both these phenomena limit the significance of the results, as has been shown by many authors (e.g. BĒRZIŅŠ 1958, TONOLLI 1958, SCHRÖDER 1959, 1962 a and b, 1964, NAUWERCK 1963, the discussion given by LÖTMARKER 1964, pp. 133—136, and the literature cited by them).

III. Composition of zooplankton samples

The following list gives the genera and species identified. Most of these are benthic. Where only the genus was identified, it is possible that more than one species of the genus was present.

Rotatoria:

Trichotria pocillum (Müll.)
Platyias
Brachionus
Mytilina
Euchlanis
Keratella cochlearis (Gosse)
" *hiemalis* (Carlin)
Kellicottia longispina (Kellicott)
Lepadella
Monommata
Trichocerca
Asplanchna priodonta Gosse
Synchaeta
Polyarthra vulgaris Carlin
" *major* Burckhardt
" *dolichoptera* Idelson
Ploesoma hudsoni (Imhof)
Filinia
Sinantherina socialis (L.)
Conochilus hippocrepis Schrank
" *unicornis* Rousselet

Cladocera:

Limnosida frontosa Sars
Diaphanosoma brachyurum (Liévin)
Holopedium gibberum Zaddach
Daphnia cristata Sars
Scapholeberis mucronata (Müll.)
Simocephalus vetulus (Müll.)
Ceriodaphnia reticulata (Jurine)
Bosmina coregoni Baird s.l.
" *longirostris* (Müll.)
Ophryoxus gracilis Sars
Eurycercus lamellatus (Müll.)
Camptocercus lilljeborgi Schoedler
Acroperus harpae Baird
Rhynchotalona rostrata (Koch)
Graptoleberis testudinaria (Fischer)
Alonella
Pleuroxus trigonellus (Müll.)
Chydorus sphaericus (Müll.)
Polyphemus pediculus (L.)

Copepoda: *Heterocope appendiculata* Sars
Eudiaptomus graciloides Lillj.
Macrocyclops albidus (Jurine)
Eucyclops serrulatus (Fischer)
Cyclops
Megacyclops viridis (Jurine)
Mesocyclops leuckarti (Claus)

IV. Comparison of two sampling methods

Samples were taken with a plexiglass tube and a Ruttner sampler. The results from the simultaneous samples taken with the two methods are presented in Table 1. These are given as the total volume of the biomass at the different sites and the number of individuals (per 8 litres) of the most frequent and volumetrically important species. The values in the Table are the sums from the samples taken at the dates indicated. The values at site 4, sampled with a Ruttner sampler, are calculated values for the whole water column, since at this site samples were taken at the surface, at 1 m, and at 2 m (bottom). Thus, the values for site 4 cannot be compared with one another in the same manner as the values from the other sites.

From the Table it can be seen that there is a large variation in number of animal found at different sites. The differences between the two sampling methods are irregular, though pronounced. At two of the sites the total biomass was higher when samples were taken with a plexiglass tube and

Table 1. The sum of the results from samples taken at July 10, 18, 24, Aug. 7, 14, 21, 28 and Sept. 4, 1961, at different sites.

	Site 1		Site 2		Site 3		Site 4	
	Ruttner	tube	Ruttner	tube	Ruttner	tube	Ruttner	tube
Total biomass as mm³/8 l	75	146	126	64	77	96	31	31
Individuals/8 l of the following species:								
Polyarthra major	—	—	65	85	19	9	169	123
Daphnia cristata	248	626	—	—	—	—	5	2
Scapholeberis mucronata	23	133	—	—	—	—	—	—
Bosmina coregoni+ longirostris	459	976	1,453	631	1,160	1,353	111	80
Polyphemus pediculus	405	317	—	—	—	—	—	—
Nauplii of *Calanoida*	2	6	338	333	262	248	381	288
Copepodids I—III of *Eudiaptomus graciloides*	—	—	14	3	1	2	33	21
Copepodids IV—V+ adults of *Eudiaptomus graciloides*	1	2	31	16	10	21	43	72
Copepodids I—III of *Heterocope appendiculata*	2	—	27	17	7	6	27	26
Copepodids IV—V+ adults of *Heterocope appendiculata*	3	1	17	36	14	24	7	9

at one site the same method gave a lower value than samples taken with the RUTTNER sampler. To get an idea of the significance of the values, the results of NAUWERCK (1963, p. 20—23), must be taken into consideration.

Among the species in Lake Erken the scattering was largest in *Bosmina* and *Daphnia,* lesser in *Cyclops* and *Eudiaptomus,* and least in *Diaphanosoma.* Thus, of the possible explanations of the observed results in Hyttödammen, the most probable one is that the results are due to swarms. It is most likely that this formation of swarms overshadows the possible effect of the different environmental factors at the different sites (see ARNEMO 1964) and the possible heterogeneity in the distribution of fish, resulting in a differing effect of predation by fish. The formation of swarms is also probably more pronounced in a pond with many biotopes owing to the presence of vegetation and the heterogeneity in its qualitative and quantitative distribution. NORDQUIST (1921) observed that qualitative differences existed over small distances when comparing a sample taken outside the vegetation in a small area of open water with samples taken closer to and in the vegetation.

To get some idea of the significance of the values in Table 1, the standard deviation was calculated for the values of the number of ind./l. found by means of the RUTTNER sampler divided by the number found with the plexiglass tube. This calculation was made for the two most numerous groups, *Bosmina* and *nauplii* of *Calanoida* on each of the 8 occasions of parallel sampling at each of the sites 1, 2 and 3. The following values were obtained:

	mean	standard deviation	range
Bosmina	2.1	2.8	0.02—12.4
nauplii of *Calanoida* ...	1.1	1.8	0.5 — 2.3

From these values it is clear that the scattering is so large that the data in Table 1 are of no statistical significance. It should also be noted that even if the sums in Table 1 seem to show good agreement for the *nauplii* of the *Calanoida,* the statistical treatment of the material indicates a large variation.

In spite of the effect of formation of swarms upon the results from sites 1, 2 and 3 when the two methods are compared, the results from site 4 as total biomass do not seem to show any influence of such an effect. However, when considering the numbers of the different species, variations are noted, probably due to formation of swarms.

Thus nothing can be proved about the validity of the two sampling methods, except for *Daphnia cristata* and *Scapholeberis mucronata* at site 1, as can be seen on p. 227—229.

V. Temporal succession and spatial distribution of zooplankton

In this section, some notes about the different species will be included. The proportions of the three main groups, *Rotatoria, Cladocera* and *Copepoda* as well as the total standing crop, will be dealt with on p. 251—261. As the higher aquatic vegetation is dominated by *Sagittaria sagittifolia* L. (see ARNEMO och NORLIN 1962 for vegetation map), only the influence of the whole vegetation upon the zooplankton will be analyzed and not the influence of the different species.

In the Figures the number of observed individuals of the different species of *Cladocera* includes young and adult animals. The different copepodid stages of *Copepoda* have been separated into only two groups, copepodids I—III and IV—V.

1. Rotatoria

The list of observed rotifers is not large, especially when compared with that of BĒRZIŅŠ (1950) for Aneboda. However, BĒRZIŅŠ made special collections for studying the benthic rotifers. In any case, the rotifers are of no significance as fish food and will therefore be treated only briefly.

All the observed *Rotatoria,* except those species occurring only in the winter, have been found both among the vegetation and in open water. The possible inhibitory effect of the higher aquatic vegetation upon the total number of individuals of *Rotatoria,* reported by HASLER and JONES (1949), can not be verified in the present investigation, as about the same number of organisms were found within and outside the vegetation areas. The results obtained in the present investigation do not exclude the validity of antagonistic action as found by HASLER and JONES. However, one has to consider the possibility that various plant species will affect rotifer species unequally. In one environment the possible antagonistic action upon some species of rotifers might be overshadowed by a non-antagonistic action upon other species of rotifers.

The systematic order in the following description of the occurrence of the species follows VOIGT (1957).

Brachionidae

Trichotria pocillum was found very rarely late in August.

Platyias occurred very rarely in August.

Brachionus was present in about 10 % of the samples with a frequency of 1—2 ind./l. from July to October.

Mytilina was found very rarely from June to September.

Euchlanis occurred as often as *Brachionus* from June to December.

Keratella cochlearis was present throughout the year (Fig. 2), but often there were only a few individuals present. The conditions seem to be better at site 1, judging from the higher numbers of individuals found there. This may be due to the presence of Dalälv water, as suggested by the distribution shown in Fig. 3 (showing the horizontal distribution) for August 2, 1962, but this is not certain. No stratification was seen in the vertical distribution at site 4 and no pronounced maxima occurred regularly in the years of investigation. Eggs were noticed throughout the year. As reported by BĒR-

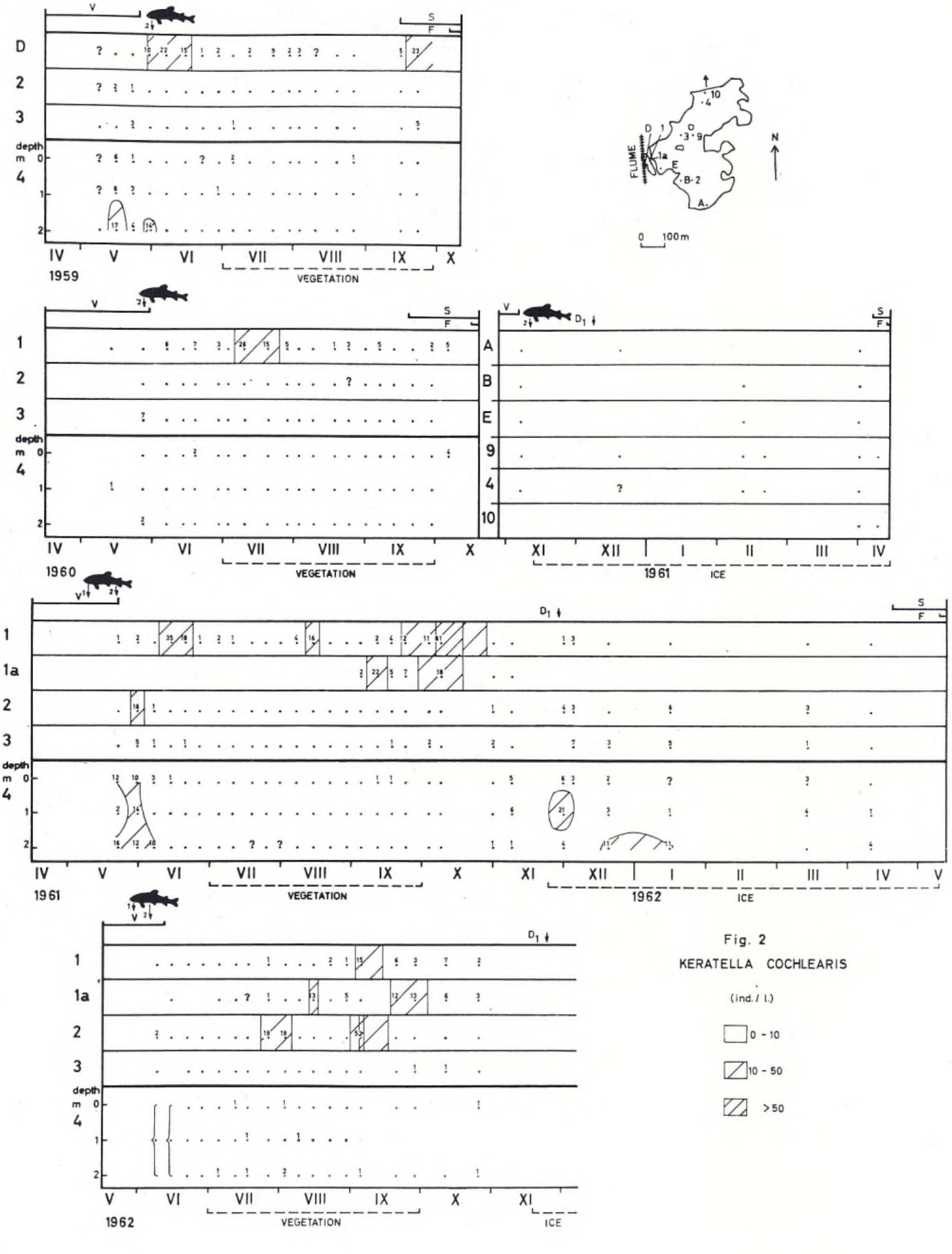
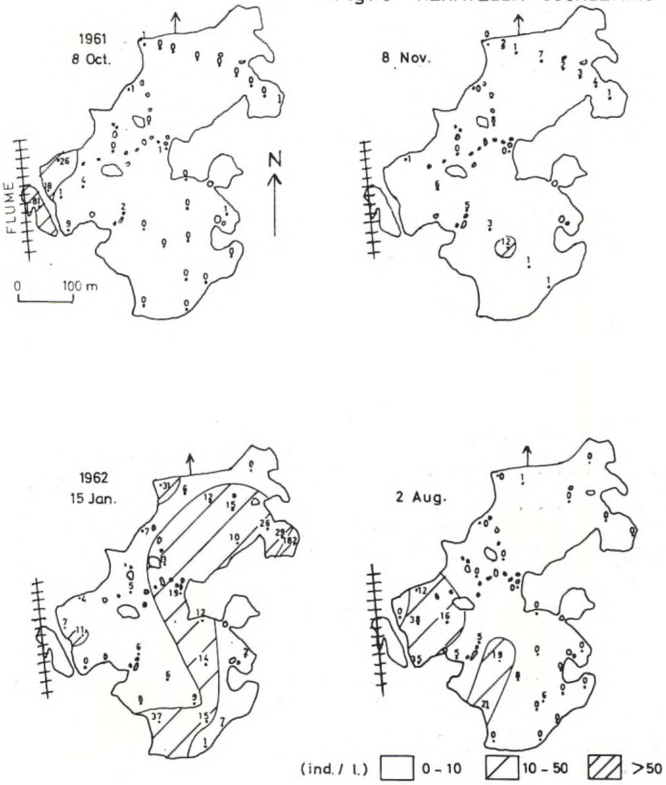


Fig. 2
KERATELLA COCHLEARIS

ZIŅŠ (1950), PEJLER (1957 a, b, 1961, 1962, 1965), AXELSON (1961), NAUWERCK (1963), this species is widely distributed in lakes and ponds in Sweden even at high latitudes. In the literature cited the quantities of the species are larger than what was found in Hyttödammen. *Keratella coch-*

Fig. 3 KERATELLA COCHLEARIS



learis was more common in 1961, and to some extent also in 1962, than in the other years.

Keratella hiemalis occurred very rarely in the winter.

Kellicottia longispina was found very rarely in three of the four years of investigation, as seen in Fig. 4. From the time of the filling of the pond in 1961 until July the numbers were somewhat higher but they never reached the numbers found in Swedish lakes (AXELSON 1961, NAUWERCK 1963). The species was observed at the same time as maximum occurred in Lake Erken. PEJLER (1957 a) never observed this species in pools and ponds, and he did not find it in the shallow Ösbysjön (1961). In 1961 *Kellicottia* was more common than in the other years.

Lepadella was found from July to October as often as was *Brachionus* and *Euchlanis*.

Notommatidae

Monommata occurred somewhat more commonly than *Brachionus, Euchlanis* and *Lepadella* with a frequency of 1—5 ind./l. from July to October, with a slight maximum late in August.

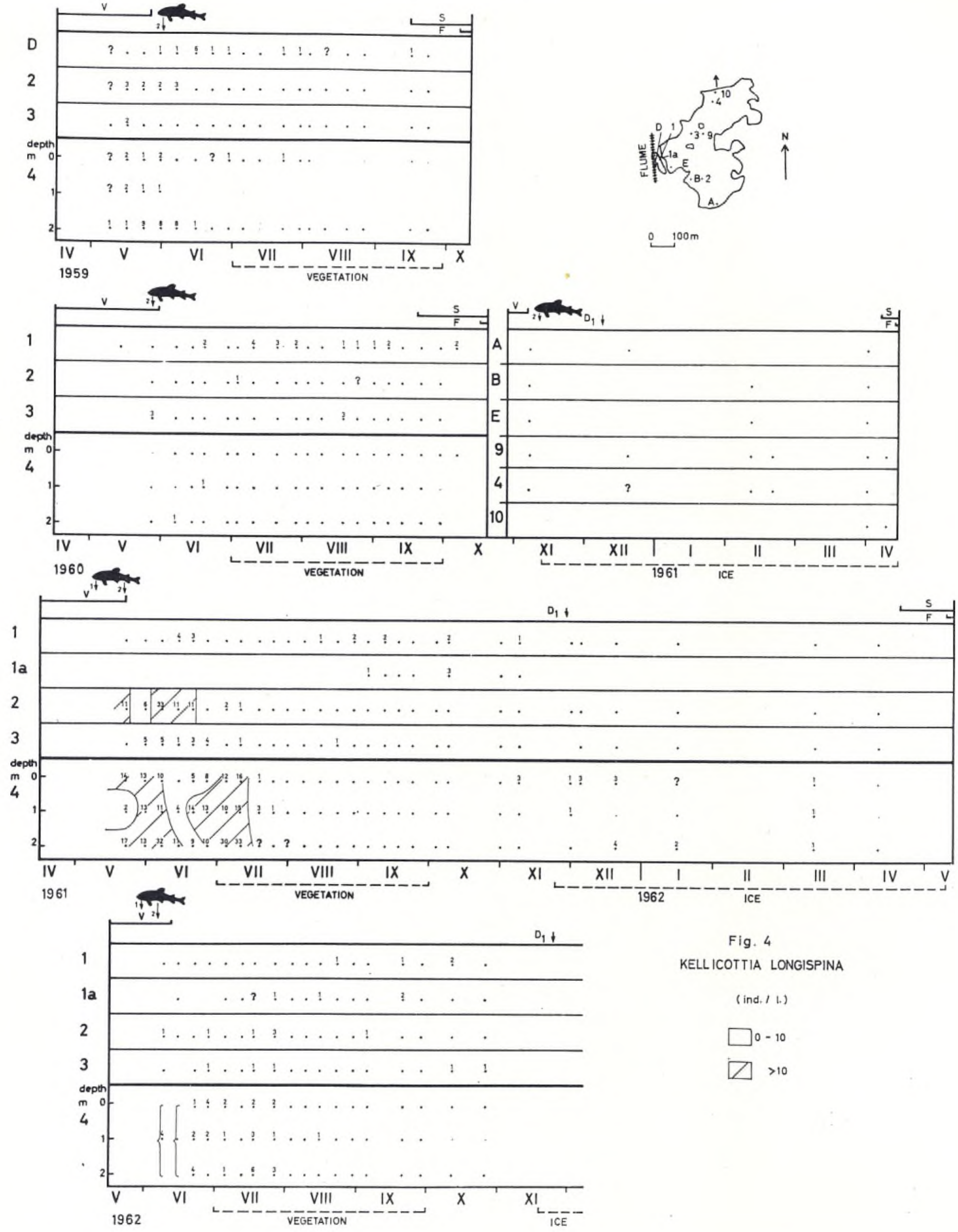


Fig. 4
KELLICOTTIA LONGISPINA
(ind. / l.)

Trichocercidae

Trichocerca was present in about 25 % of the samples with a frequency of 1—5 ind./l. and sometimes up to 15 ind./l. from July to October.

Asplanchnidae

Asplanchna priodonta (Fig. 5) was found in the highest numbers after

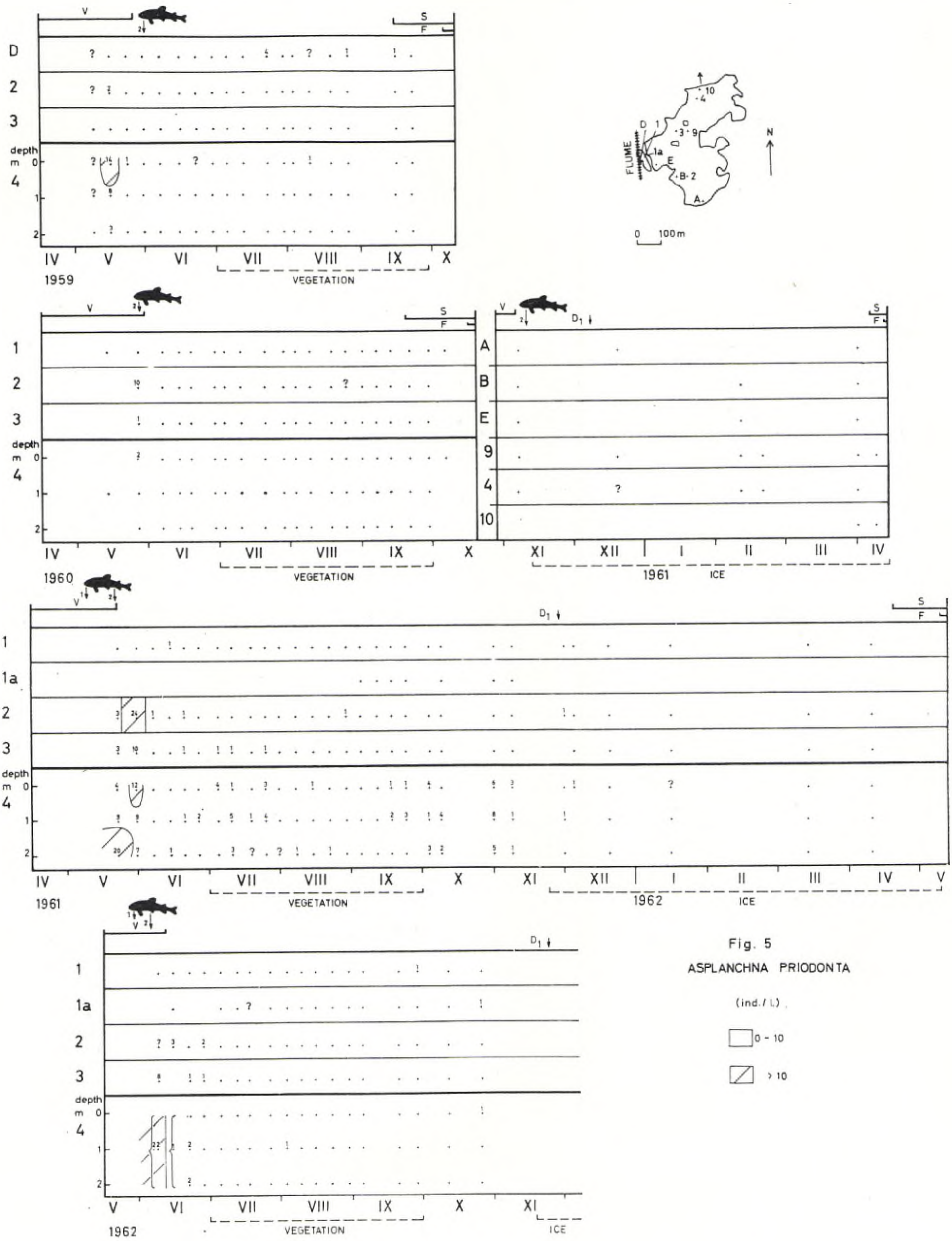


Fig. 5
ASPLANCHNA PRIODONTA
(ind./L.)

the filling of the pond in May and in the beginning of June. The numbers are slightly lower than those found by PEJLER (1961) and NAUWERCK (1963).

Synchaetidae

Synchaeta (Fig. 6) occurred in May and from October to January. *Synchaeta* shows together with *Polyarthra spp.,* the highest numbers of the

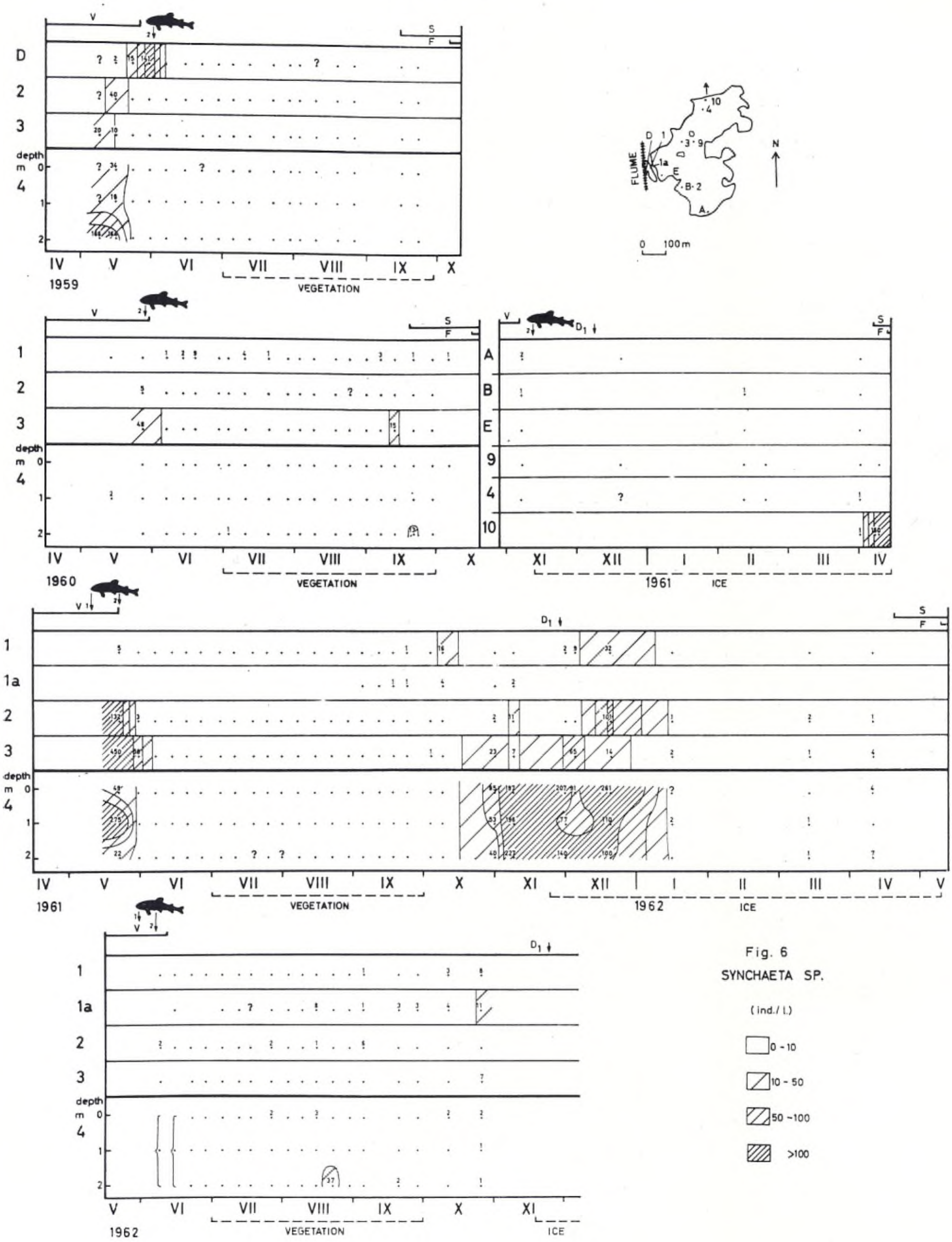
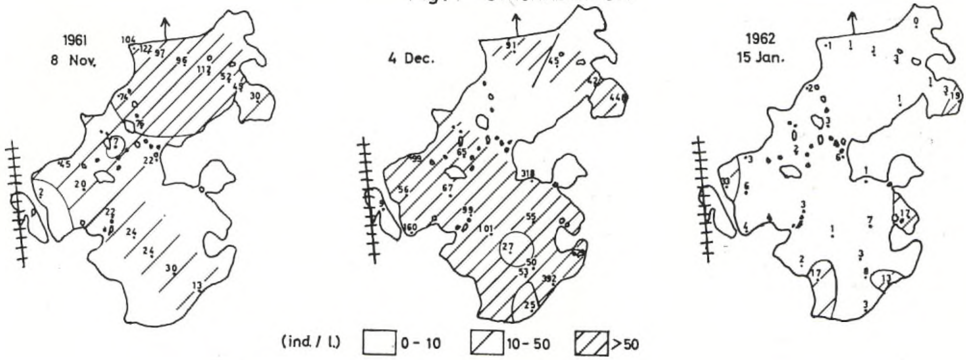


Fig. 6
SYNCHAETA SP.

rotifers. In the winter of 1960/61 *Synchaeta* was lacking. This may have been due to the draining of the pond in October 1960. The resting eggs may have been mostly destroyed then, and when the pond was filled at the beginning of November the few individuals could not give rise to populations as large as those found in the following winters.

Fig. 7 SYNCHAETA SP.



NAUWERCK (1963) found *Synchaeta oblonga* and *S. truncata* from December to May, with a maximum in the end of January. PEJLER (1961) found a maximum of *S. pectinata* and *S. truncata* in May-June in the small Ösbysjön. Hyttödammen differs from these in that one maximum occurred in November-December (1961) and another shorter one in May (1961). The horizontal distribution in Fig. 7 showed the highest values close to the shore in December 4, 1961. By January 15, 1962 the population had almost died out. Somewhat higher values were to be found close to the shore even at that date.

Polyarthra was represented by the species *P. vulgaris, P. major* and *P. dolichoptera.* These species were only differentiated from one another in samples taken from the time of the filling of the pond in spring 1960 to the beginning of November 1961. The distribution of the species during that time can be seen in Figs. 8—10. The sum of the three species is given in Fig. 11. In Fig. 12 are given the horizontal distribution of the most common species during the summer, of *P. major,* and the sum of the three species.

From Fig. 8 it can be seen that *P. vulgaris* was to be found in low quantities in the summer. *P. major* in Fig. 9 was more common and had higher values in areas free from vegetation. This tendency was also found in Fig. 12, especially on August 28, 1961. No vertical stratification in the distribution was found. *P. dolichoptera* in Fig. 10 was to be found in low quantities and almost only at site 1, perhaps favourably influenced by the Dalälv water.

As is seen in Fig. 11, the sum of the three species was high in the summer at site 1 (*P. dolichoptera*) and at sites 2, 3 and 4 *(P. major*) and in the winter throughout the pond (probably *P. vulgaris*). As was the case with *Synchaeta,* the highest values were found close to the shore, for example on January 15, 1962. The observations of the temporal distribution

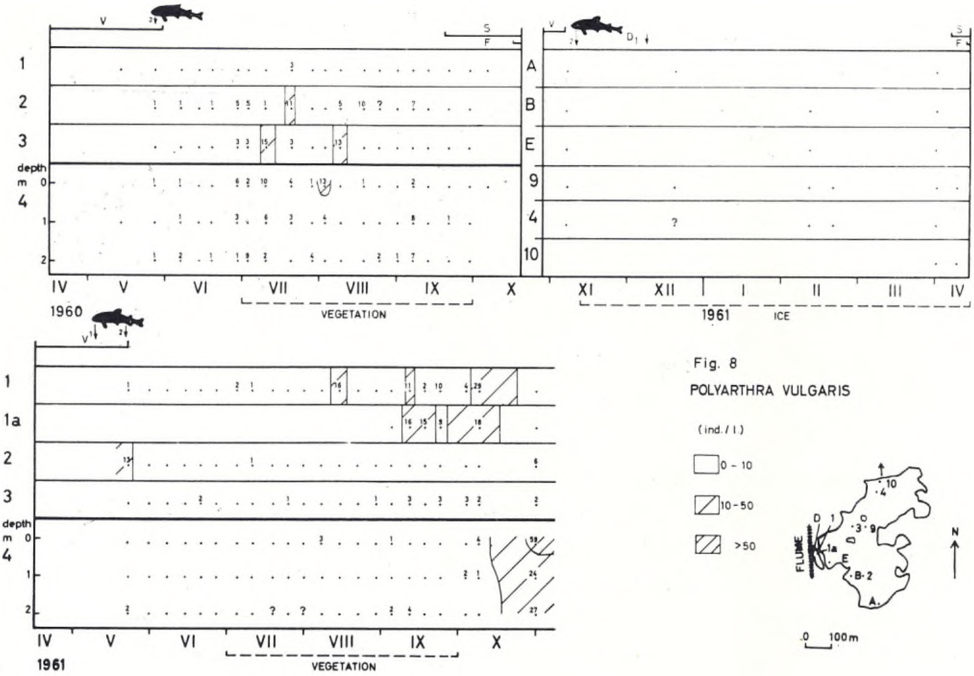


Fig. 8
POLYARTHRA VULGARIS

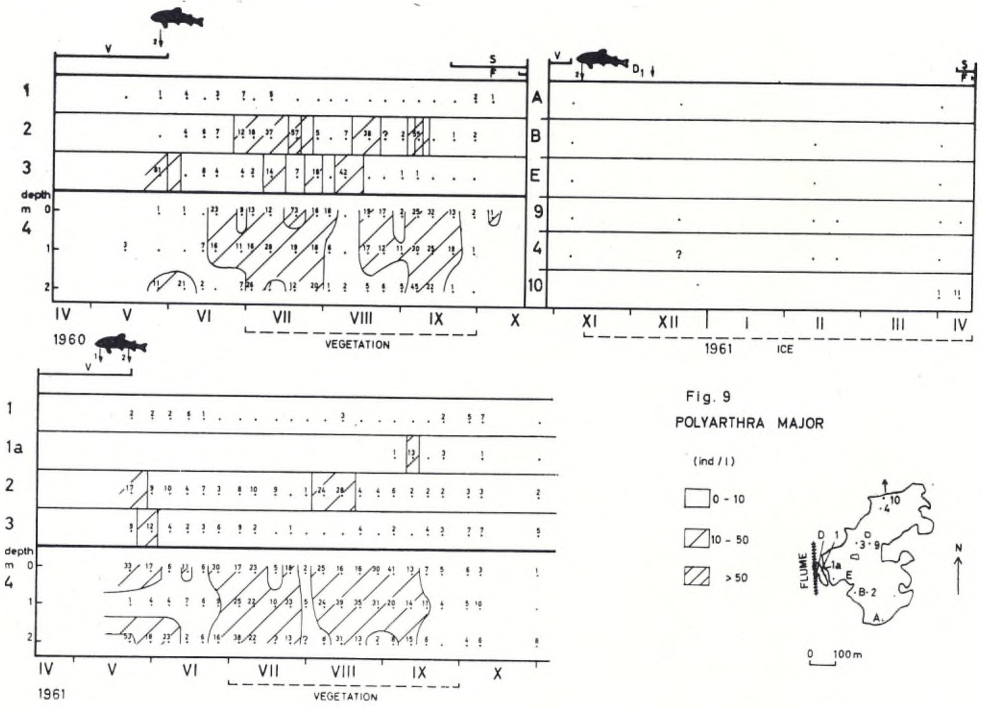


Fig. 9
POLYARTHRA MAJOR

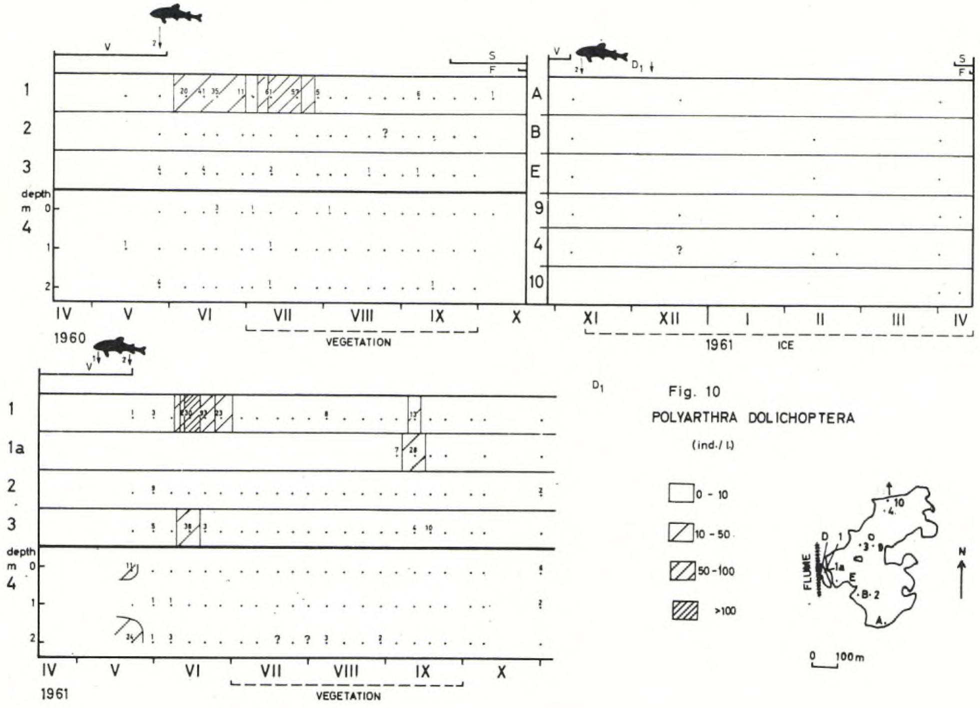


Fig. 10
POLYARTHRA DOLICHOPTERA
(ind./l.)

of *P. major* agree with those by **Pejler** (1961) in the small Ösbysjön. **Nauwerck** found it only rarely in Lake Erken. In 1959—61 the temporal distribution of *P. major* at site 4 was about the same as in Lake Erken, but in 1962 it was present for a somewhat shorter time.

P. dolichoptera is considered as a cold-water form (see references given by **Pejler** 1961 and observations by **Nauwerck** 1963). However, **Pejler** also found it in the summer at temperatures of 18—19°C, and the temperature conditions were the same at site 1 when *P. dolichoptera* was found. (Cf. **Arnemo** 1964, pp. 19—20.) The number of ind./l. was very low in 1962 at site 1, and the maximum in 1960 was not as high as in 1959 and 1961.

P. vulgaris was found by **Carlin** (1943) to be common in summer and rare in winter. **Pejler** (1957 a and b) found it throughout the year. The two authors cited found it to be one of the commonest rotifers. In late winter **Pejler** found a decrease caused by too low a concentration of oxygen. In Hyttödammen the oxygen concentration might also be the factor that reduces the population, though the oxygen content never reaches zero. **Pejler** (1956) found that *P. vulgaris* avoided low oxygen levels. The numbers in Hyttödammen were about the same order of size as those of the cited authors.

Ploesoma hudsonii was found, though but rarely, in August.

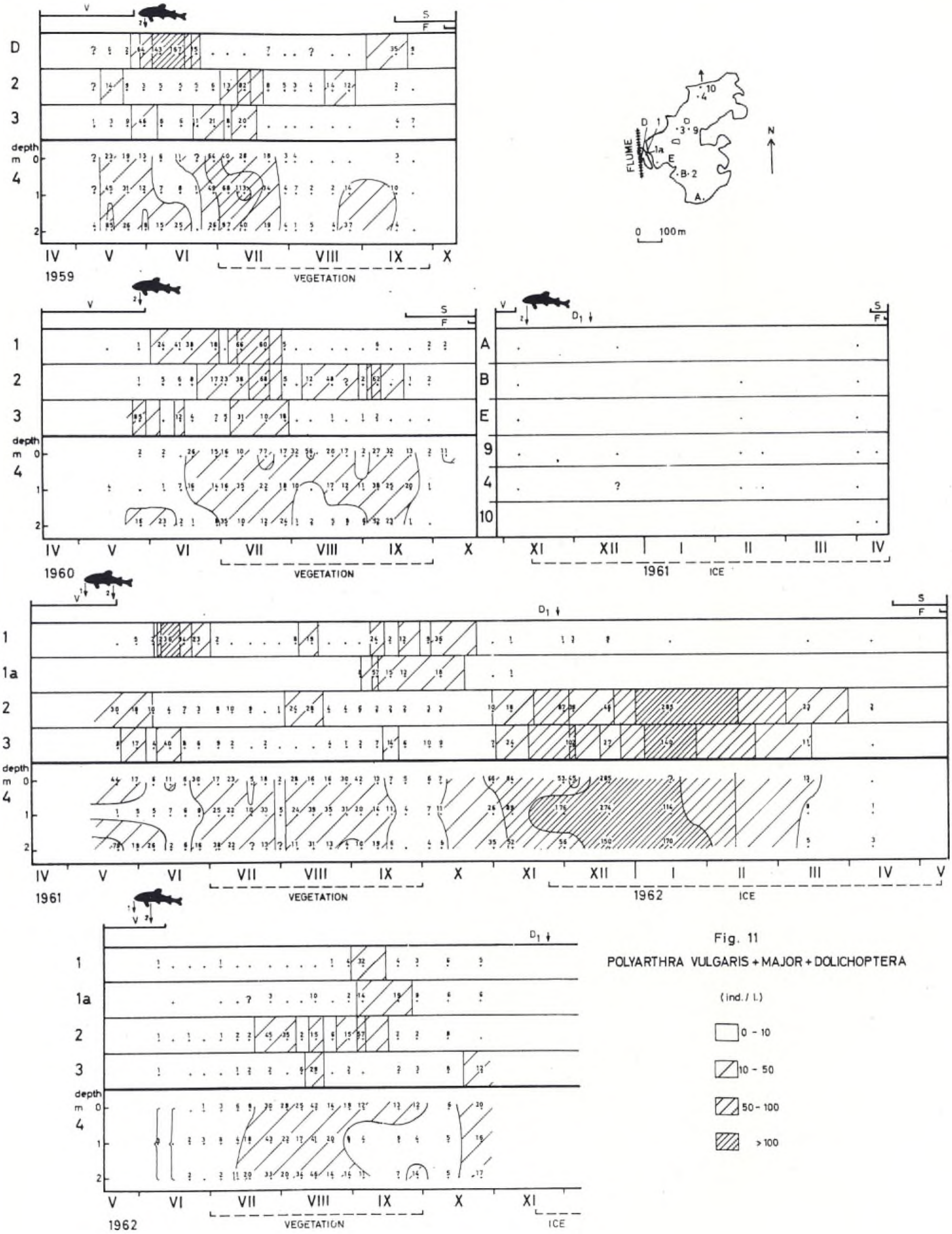


Fig. 11

POLYARTHRA VULGARIS + MAJOR + DOLICHOPTERA

(ind. / l.)

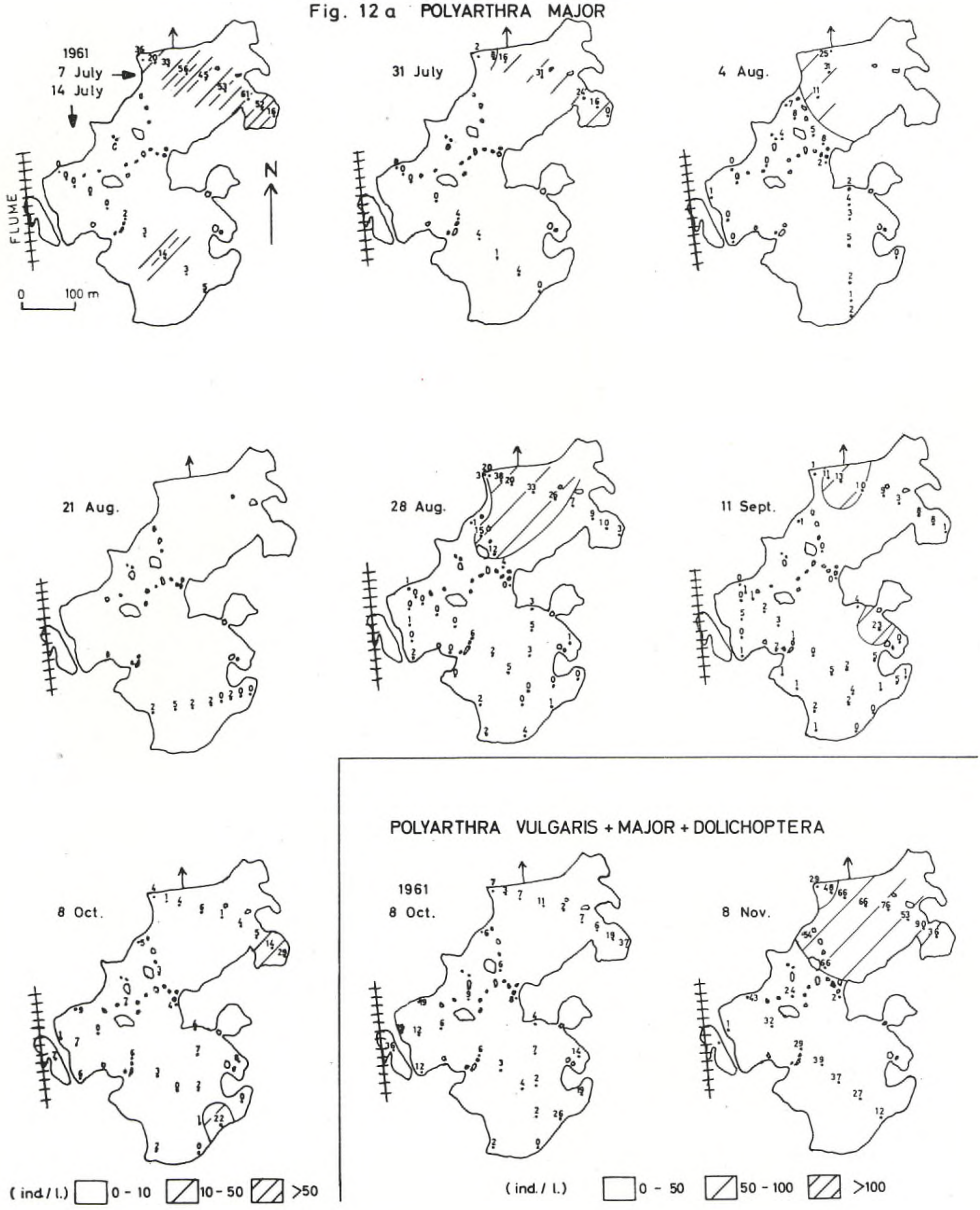
Testudinellidae

Filinia occurred, though but rarely, in August.

Flosculariidae

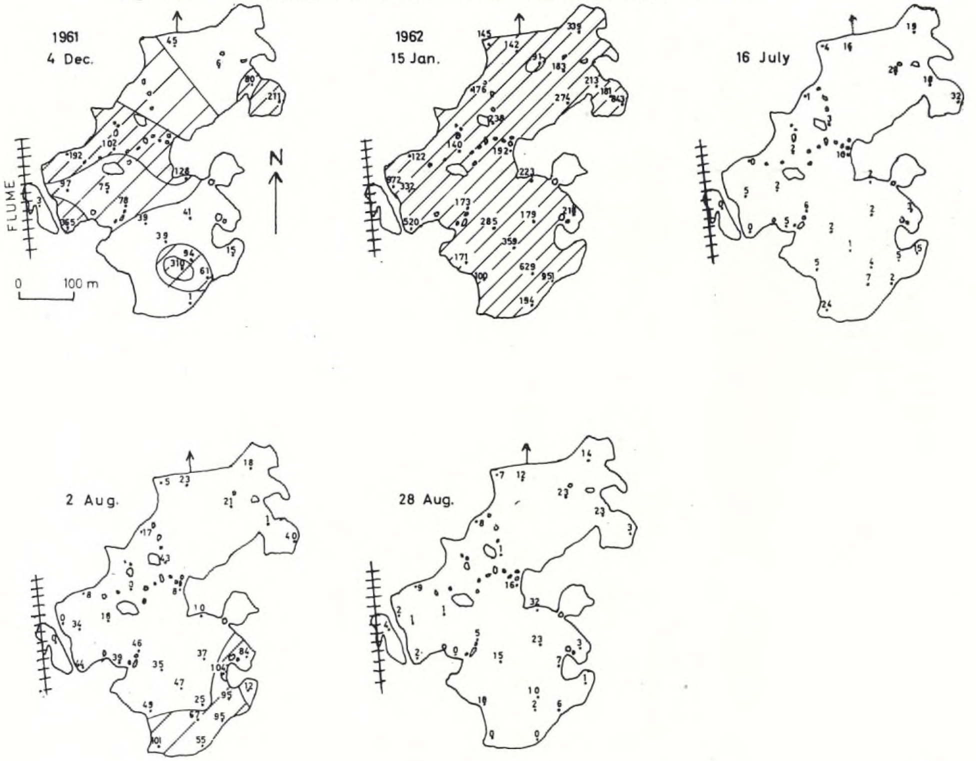
Sinantherina socialis (determined by Dr. B. BERZIŅŠ) was found in varying abundance during the whole summer (Fig. 13). Judging from the ver-

Fig. 12 a POLYARTHRA MAJOR



tical distribution of the species it is apparent that *Sinantherina socialis* lives near the bottom. This is also emphasized in the results from a series of samples taken at four-hour intervals on September 1 and 2, 1961. The values indicate the number of ind./l.:

Fig. 12 b POLYARTHRA VULGARIS + MAJOR + DOLICHOPTERA cont'd.



Time	Depth m 0	1	2
0600	–	–	538
1000	1	–	406
1400	2	4	144
1800	1	2	467
2200	–	1	235
0200	3	2	–

From this it can also be seen that the species occurred in a thin layer close to the bottom. This layer might at times be missed by sampling, giving the impression of a rapid population decrease.

As this colonial species is sometimes free-swimming and sometimes attached, its inclusion in considering zooplankton might be questioned. However, in the present article, all the observed species, even the benthic, have been added together to obtain the total standing crop of zooplankton. The somewhat haphazard sampling of the benthic organisms did not allow isopletes to be drawn in Fig. 13.

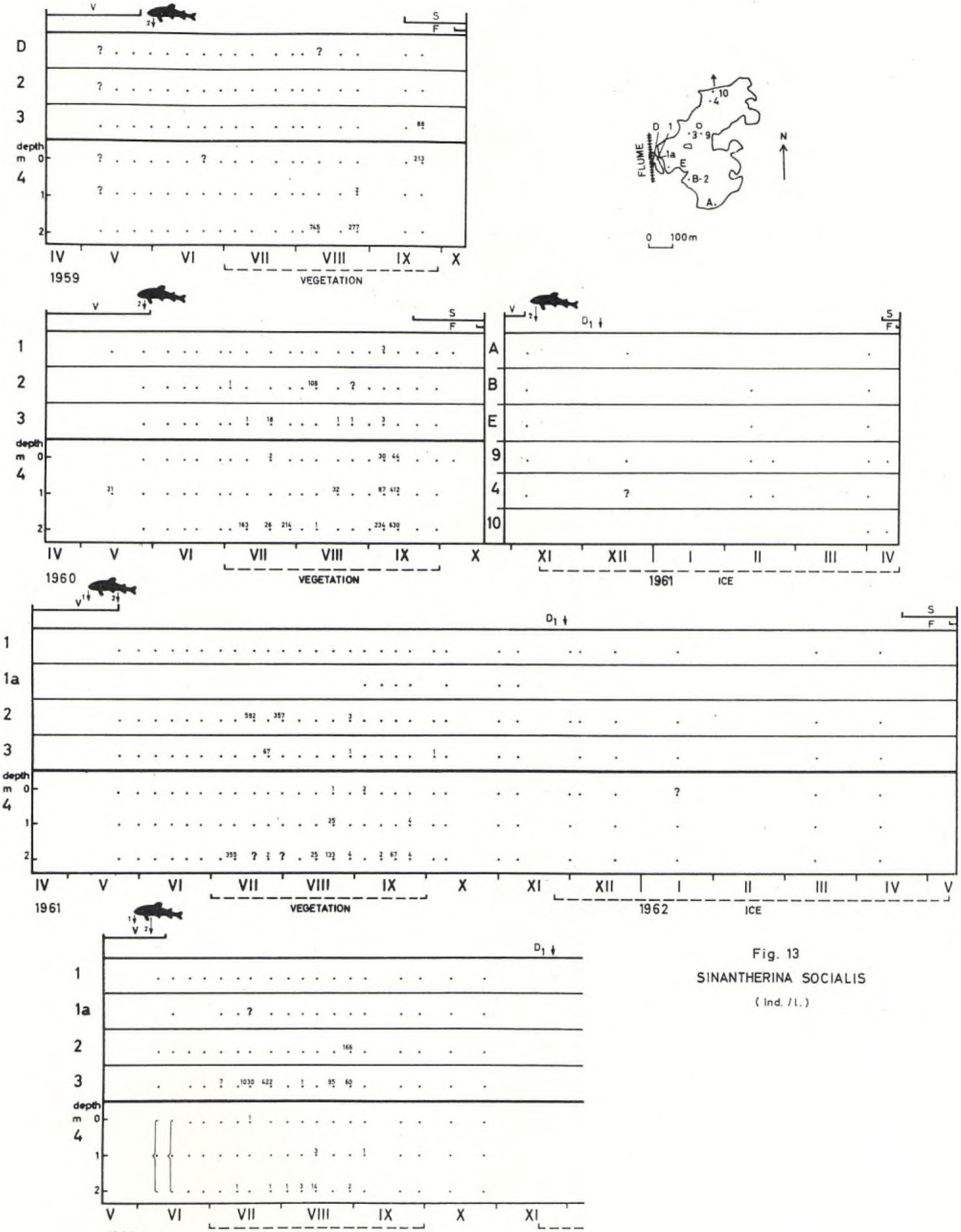


Fig. 13
SINANTHERINA SOCIALIS
(Ind. / l.)

Conochilidae

Conochilus hippocrepis and *C. unicornis* are added together in Figs. 14 and 15. These two species are colonial plankters. They were found from June to October. The numbers in September and October were much lower than in the other months. The time and the magnitude of the maxima vary

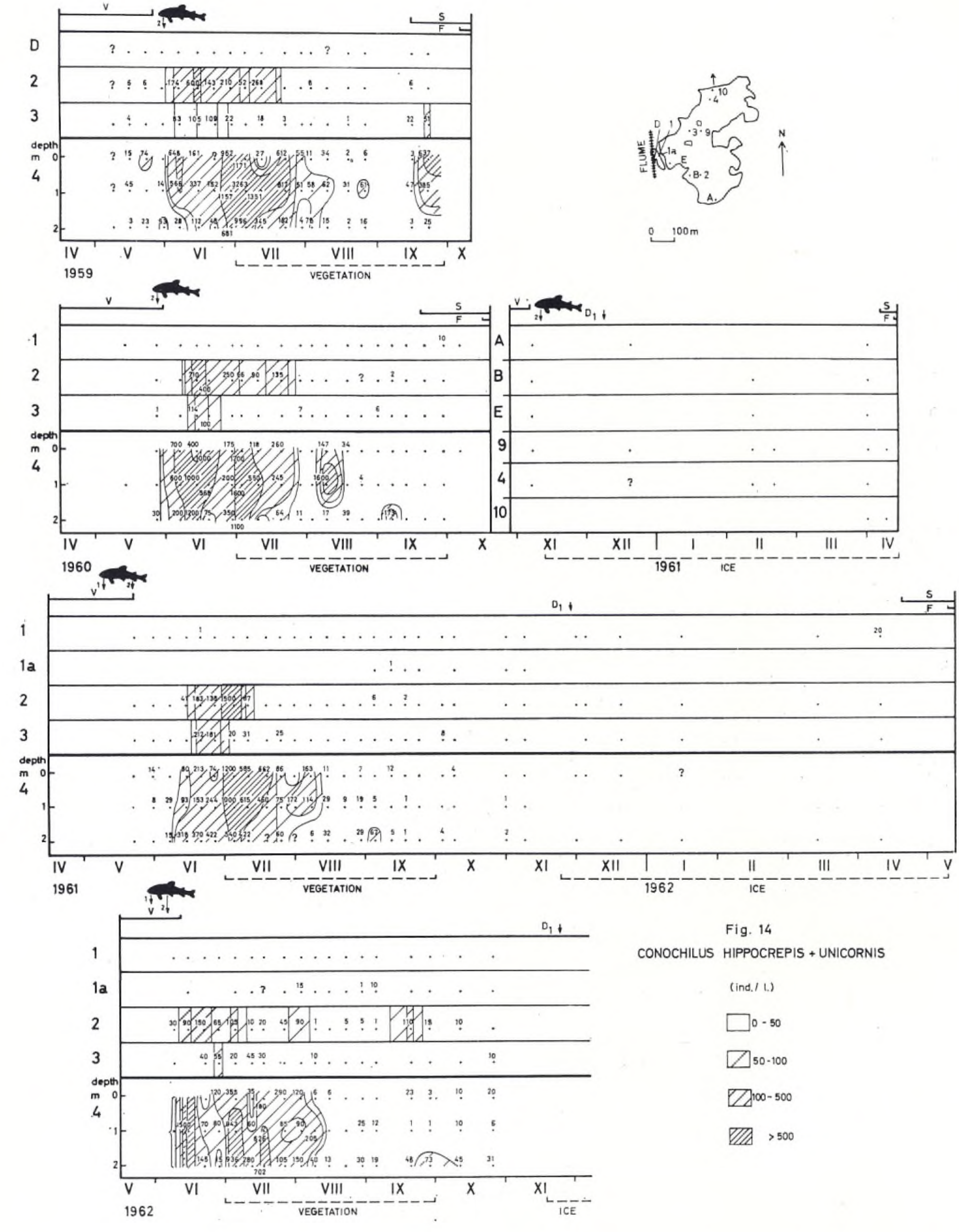
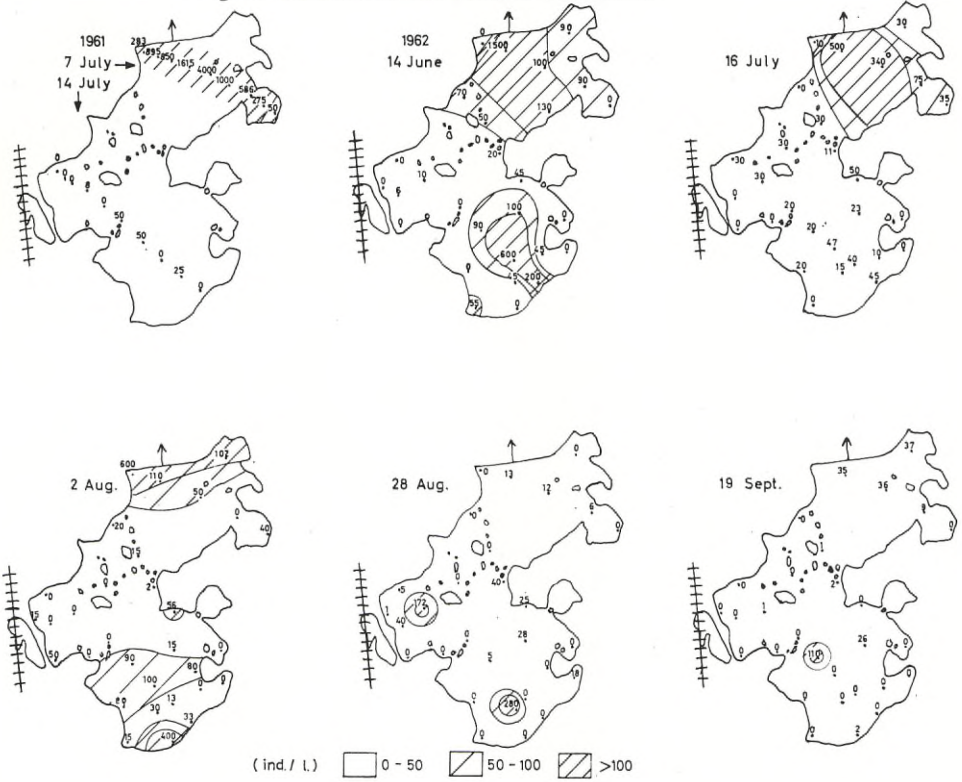


Fig. 14
CONOCHILUS HIPPOCREPIS + UNICORNIS
(ind./l.)

from year to year. The number of ind./l. are higher than Pejler (1957 a) and Nauwerck (1963) found. Pejler (1957 b) did not find *C. unicornis* in any small lakes and ponds in central Sweden. The observations in the present investigation agree with Carlin-Nilsson (1935) in his investigations of the ponds at Aneboda. In Fig. 15 it can be seen that the vegetation did

Fig. 15 CONOCHILUS HIPPOCREPIS + UNICORNIS



not influence the horizontal distribution of these species. However, they never occurred in high numbers in the part of the pond where the Dalälv water enters.

2. Cladocera

Limnosida frontosa was found very rarely in July 1962. It is usually considered to be distributed only in the pelagic zone (SARS 1865, LILLJEBORG 1900) but the few individuals in Hyttödammen were found both within and outside the vegetation. GRIMÅS *et al.* (1954) found it only rarely in the ponds at Bergeforsen.

Diaphanosoma brachyurum (Fig. 16) was found from May to September in low numbers. No significant vertical distribution and no differences in occurrence between the years were found. The horizontal distribution in Fig. 17 shows that the higher values are found both in 1961 and 1962 within and in the vicinity of the small bay in the south-eastern part of the pond. Perhaps this irregularity in the distribution is due to the environment (see ARNEMO 1964, pp. 39—40 and Fig. 18).

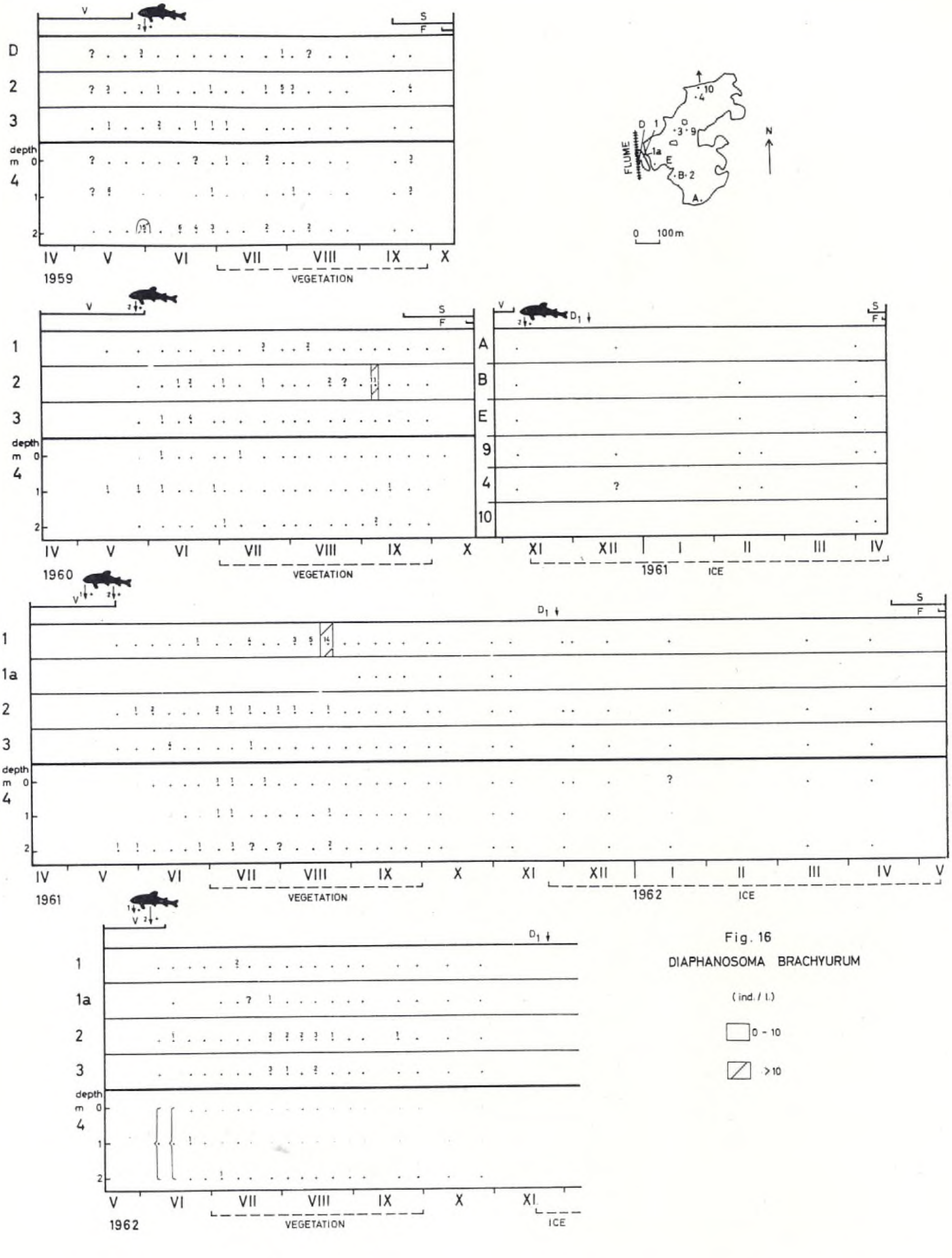
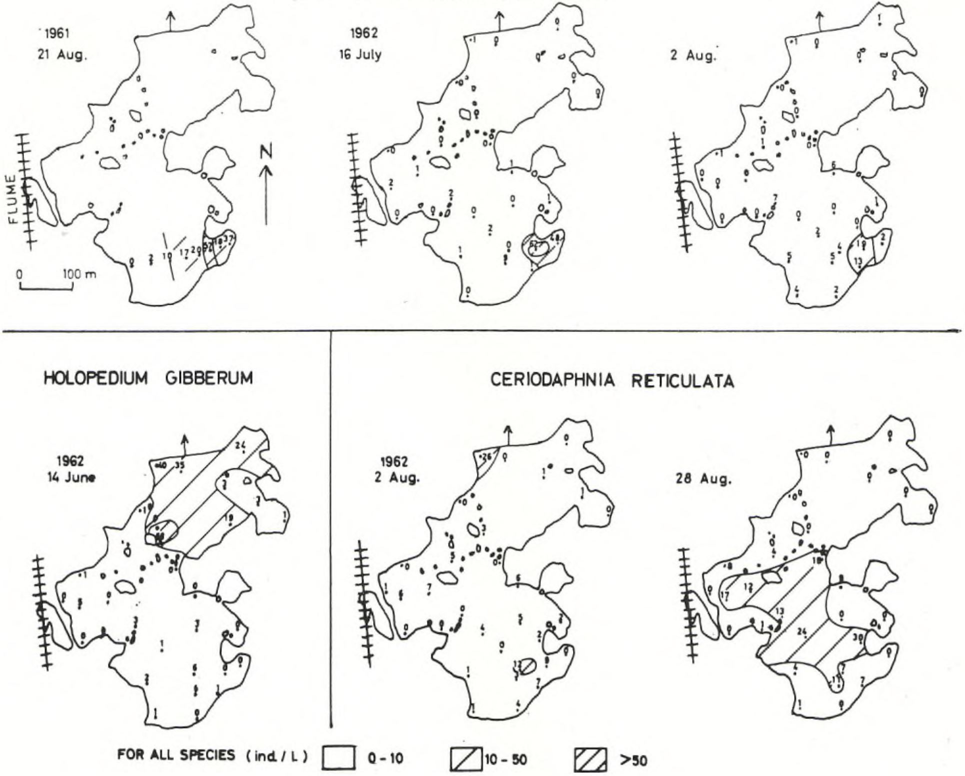


Fig. 16
DIAPHANOSOMA BRACHYURUM
(ind./l.)

The number of ind./l. are much lower than those found by NAUWERCK (1963) in the epilimnion in Lake Erken, but are similar to the observations by GRIMÅS *et al.* (1954), and PEJLER (1961, 1962) for small lakes and ponds. NORDQUIST (1921) found it to be sub-dominant in eutrophic and oligotrophic ponds in south Sweden, and SARS (1865) mentioned that the species was

Fig. 17 DIAPHANOSOMA BRACHYURUM



distributed in low quantities in the pelagic as well as in the littoral zones. Quite contrary to the observations of Sars are those of WESENBERG-LUND (1952), who considers *D. brachyurum* a typical pelagic species, occurring even in small lakes but never within the vegetation. This last finding does not agree with the findings in Hyttödammen. The low values in Hyttödammen agree with those found in other ponds and small lakes. The species is considered to be a warm-water form, and in the small water bodies referred to above the temperature in the summer reaches high values which ought to favour the development of *D. brachyurum*. Further discussion of what may be limiting the population occurs on p. 265.

Holopedium gibberum was to be found from May to September, as seen in Fig. 18, with a maximum in June and highest numbers at site 4. This is the second most abundant *Crustacea* species, after *Bosmina*. The maximum density of the population varies from year to year at site 4. At the other sites the numbers are very low during the maximum and the species is rarely to be found (see also Fig. 17). At the time when the vegetation grows up, the population density at site 4 equals that of the other sites. With the

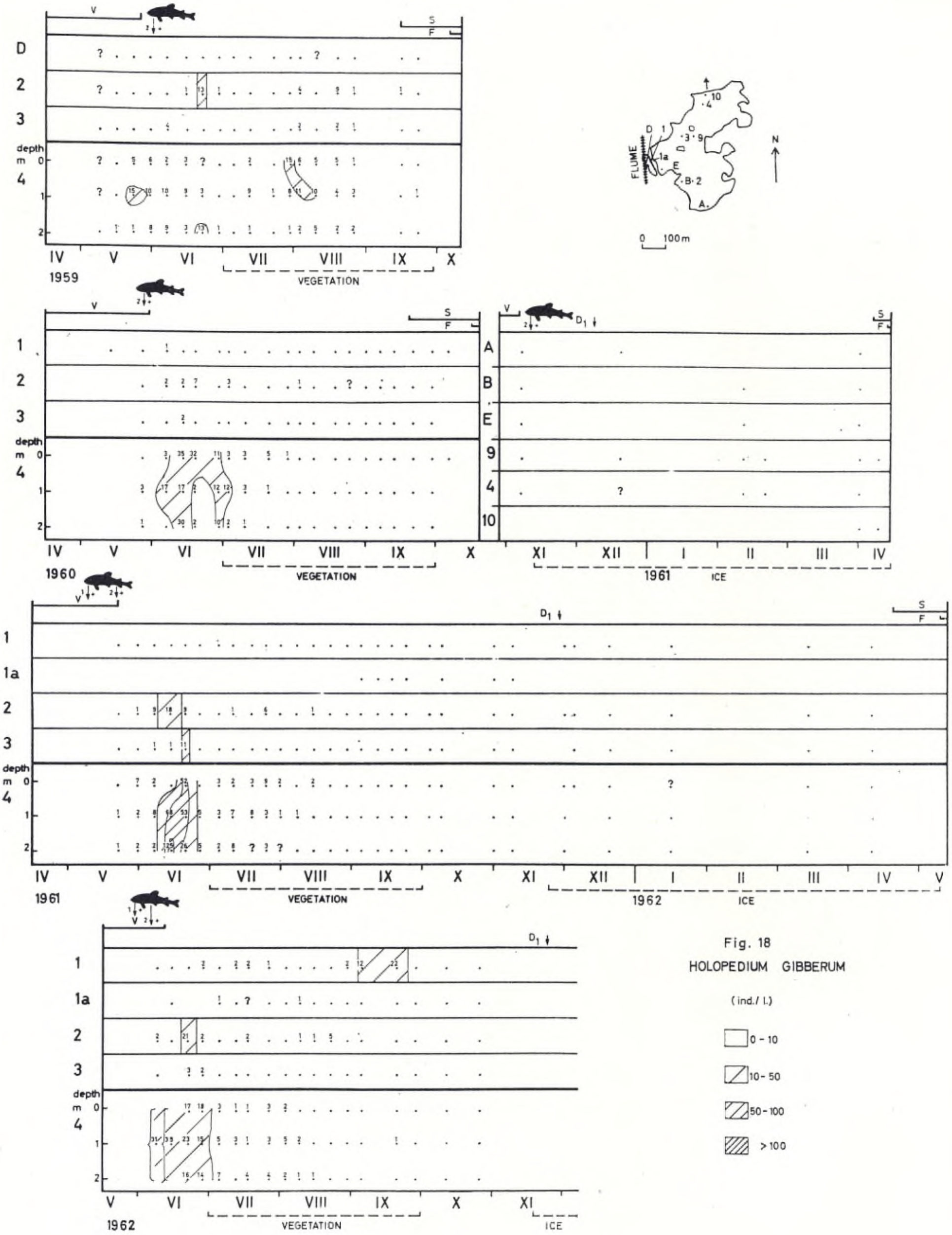


Fig. 18
HOLOPEDIUM GIBBERUM
(ind./l.)

exception of the observations at site 4, the distribution at the sites agrees with the observations of Sars (1865), Ekman (1904) and Wesenberg-Lund (1952), who found it only rarely close to the shore and in the littoral among vegetation. Site 4 is situated in the part of the pond where no vegetation is growing. However, the decrease in the population density at the other sites might be influenced by the presence of the dense vegetation.

Among the Swedish investigations giving quantitative information, PEJLER (1961, 1962) and NAUWERCK (1963) did not find *H. gibberum* in eutrophic lakes, and LINDSTRÖM (1952, 1958), GRIMÅS *et al.* (1954), AXELSON (1961) found it only in small quantities. PUKE (1949) found it in central Sweden only in waters poor in electrolytes, and PEJLER (1965) considers it to be an indicator of oligotrophy. LÖTMARKER (1964) found it to be one of the dominating species in his investigation of thirteen north Swedish lakes. FREIDENFELT (1921) gave some quantitative information from some tarns. In one of them (Oxögat) he noted a total zooplankton volume of 15.88 cm^3/m^3 at a depth of 2 m. This total was mainly *H. gibberum* which may have been at a maximum at that date. The volume is of the same order of size as the maximum found in Hyttödammen in the middle of June 1961 (mean value at site 4 on June 14: 7.15 mm^3/l). However, FREIDENFELT also found the species in samples taken on June 9, as well as on August 14 and September 16.

The differences in population development observed in Hyttödammen at site 4 in the beginning of July and in Oxögat by FREIDENFELT, seem difficult to explain. HAMILTON (1958) notes an upper limiting temperature value for survival of 25°C. Perhaps the temperature in Hyttödammen which rapidly increases to 20°C in June, determines the further development of the population, though the temperature later never reaches lethal values. THIENEMANN (1926) considered that *H. gibberum* preferred oligotrophic, calcium-poor waters. According to THIENEMANN, Hyttödammen is oligotrophic. ARNEMO and NAUWERCK (1965) found Hyttödammen to lie between oligotrophic and eutrophic *sensu* RODHE (1958). Hyttödammen is also considered to be calcium-poor, as HAMILTON (1958) gave an upper limit of 20 mg/l Ca^{++}. The values found in Hyttödammen are shown on pp. 46—47 in ARNEMO (1964). However, it is to be noted that calcium is the dominant cation.

Other factors that limit the population size and make comparisons between different environments difficult are differing competition for food and the differing influence of predation. All the factors mentioned above may be illustrated by the findings of HAMILTON (1958), who did not observe any environmental differences (7 factors) in 30 Scottish lochs, yet found *Holopedium* in only some of them.

Daphnia cristata with the three forms *D. c. cristata, D. c. longiremis* and *D. c. cederströmi* have been determined by Dr. B. BĒRZIŅŠ. *D. cristata* (Fig. 19) was found in low numbers from May to the beginning of October. At site 1 where the species was most numerous, differences seemingly exist when 1960 is compared with 1961 and 1962, but this is likely to be a result of the two sampling methods used. Table 1 plus observations in the field show that *D. cristata* was distributed close to the bottom at site 1 (depth= 0.4 m). When taking a water-column sample with a plexiglass tube the

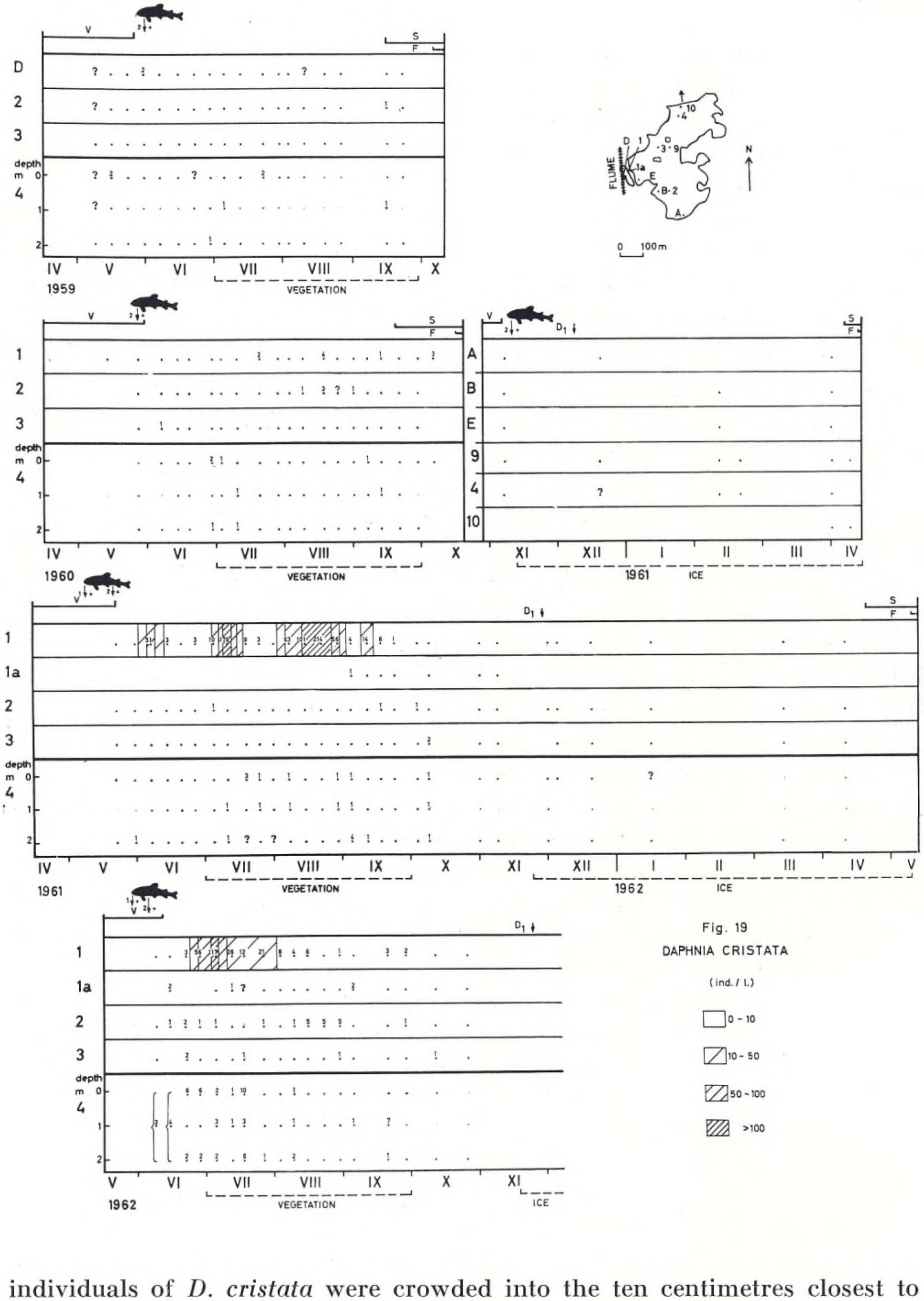


Fig. 19
DAPHNIA CRISTATA
(ind. / l.)

individuals of *D. cristata* were crowded into the ten centimetres closest to the bottom. This part of the water column can never be taken in a Ruttner sampler.

D. cristata was common in some of the lakes investigated by LÖTMARKER

(1964). However, in ponds in Sweden other species of *Daphnia* are reported by NORDQUIST (1921) to dominate the zooplankton and GRIMÅS *et al.* (1954) found *Daphnia* only a few times, so it was certainly playing a subordinate role as in Hyttödammen. Because of the low frequency of occurrence of *D. cristata* in Hyttödammen, nothing can be said about its vertical or horizontal distribution. Males were observed in September and October.

Scapholeberis mucronata was found rarely in the pond and almost exclusively at site 1. As it is considered to live in immediate contact with the surface of the water where it feeds on neuston (NAUMANN, 1921), the two sampling methods give very different results (Table 1). It is underrepresented when sampling is done with a RUTTNER sampler. This sampling problem explains the differences observed between its occurrence in 1960 from June to September in 50 % of the samples with a frequency of 1—6 ind./l. and in 1961 from July to September in 80 % of the samples with a frequency of 1—63 ind./l. GRIMÅS *et al.* (1954), in the only quantitative sampling from Sweden, found it in low numbers in few samples. NORDQUIST (1921) considers *S. mucronata* to be an oligotrophic pond form.

Simocephalus vetulus was found very rarely from July to September within and outside the vegetation. LILLJEBORG (1900) considered *S. vetulus* to be a common species in ponds and small waters, always occurring in contact with the vegetation.

Ceriodaphnia reticulata (Fig. 20) was found very irregularly at the different sites. Its sudden occurrence in high numbers probably indicates that swarms were present. It occurred from May to September, which is about the same season as that in which LILLJEBORG (1900) found the species in the vicinity of Uppsala. LILLJEBORG, the only information from Sweden about *C. reticulata,* observed it in ponds and small waters. As a rule the horizontal distribution was as shown in Fig. 17 on August 2, 1962, with no significant differences. On one occasion, August 28, 1962, somewhat higher values were found in areas with dense vegetation.

Bosmina coregoni and *B. longirostris* were the most numerous of the zooplankton in Hyttödammen. Dr. B. BĒRZIŅŠ has determined three forms of the former species, *B. c. arctica, B. c. longispina* and *B. c. obtusirostris,* and one of the latter, *B. l. pellucida.* When counting the samples no distinctions were made between the two species. Spot checks were made to get an idea of the proportions of the two species, and judging from these *B. coregoni* dominated.

From Fig. 21 it can be seen that *B. spp.* were found regularly from May to October, and rarely found throughout the winter. There is a difference in the concentration at sites 1, 2 and 3, where there is dense vegetation, compared with site 4, where there is no vegetation. This difference is also found at times when no vegetation is grown up. Maximum population density is very hard to determine because of the rapid changes of generations (cf.

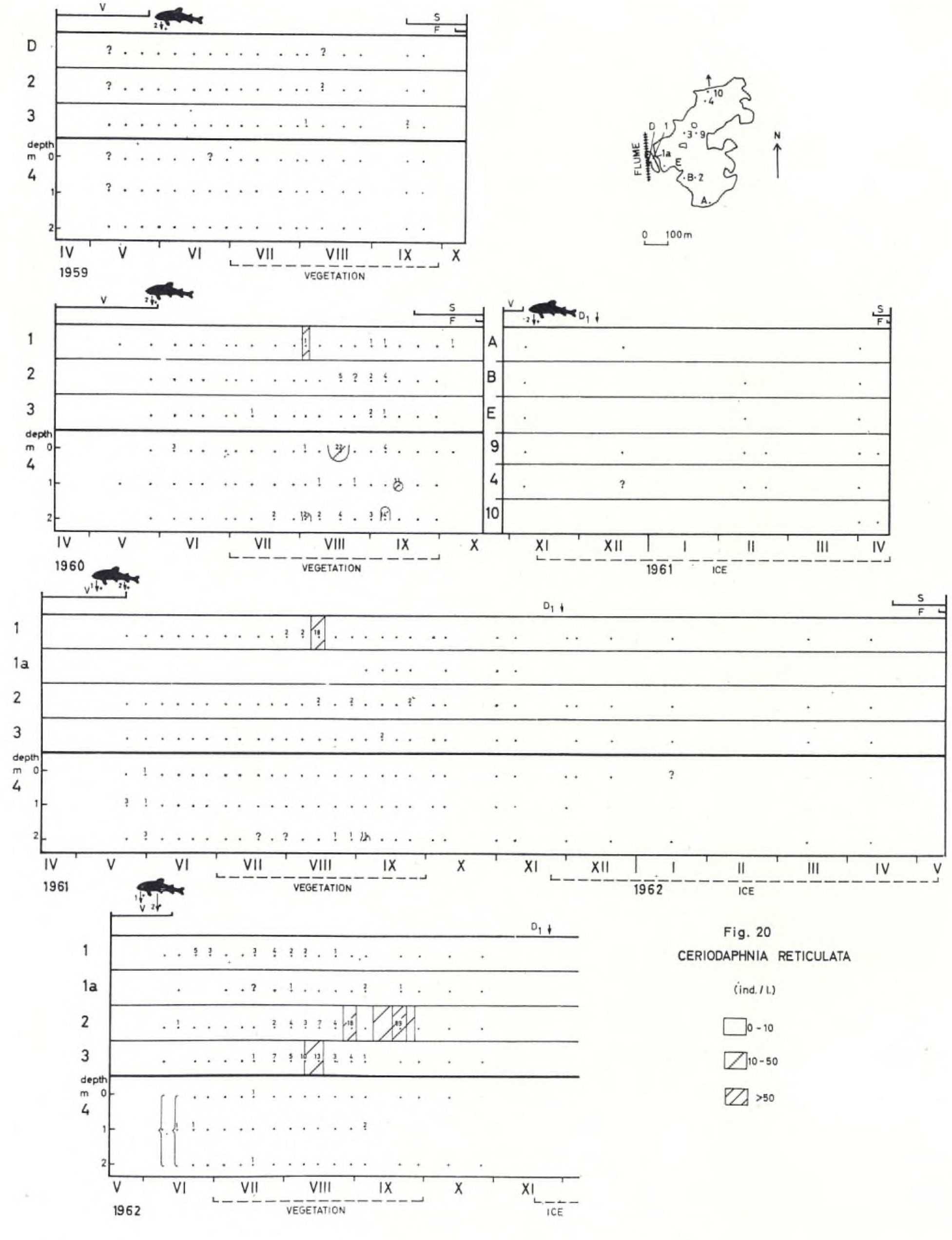


Fig. 20
CERIODAPHNIA RETICULATA

p. 260) and to some extent also becase of probable overshadowing by swarm formation. However, as a rule, it seems that several maxima occurred in July-August.

The horizontal distribution (Fig. 22) emphasizes the observations that were made above. The highest concentration observed was 1,486 ind./l. in

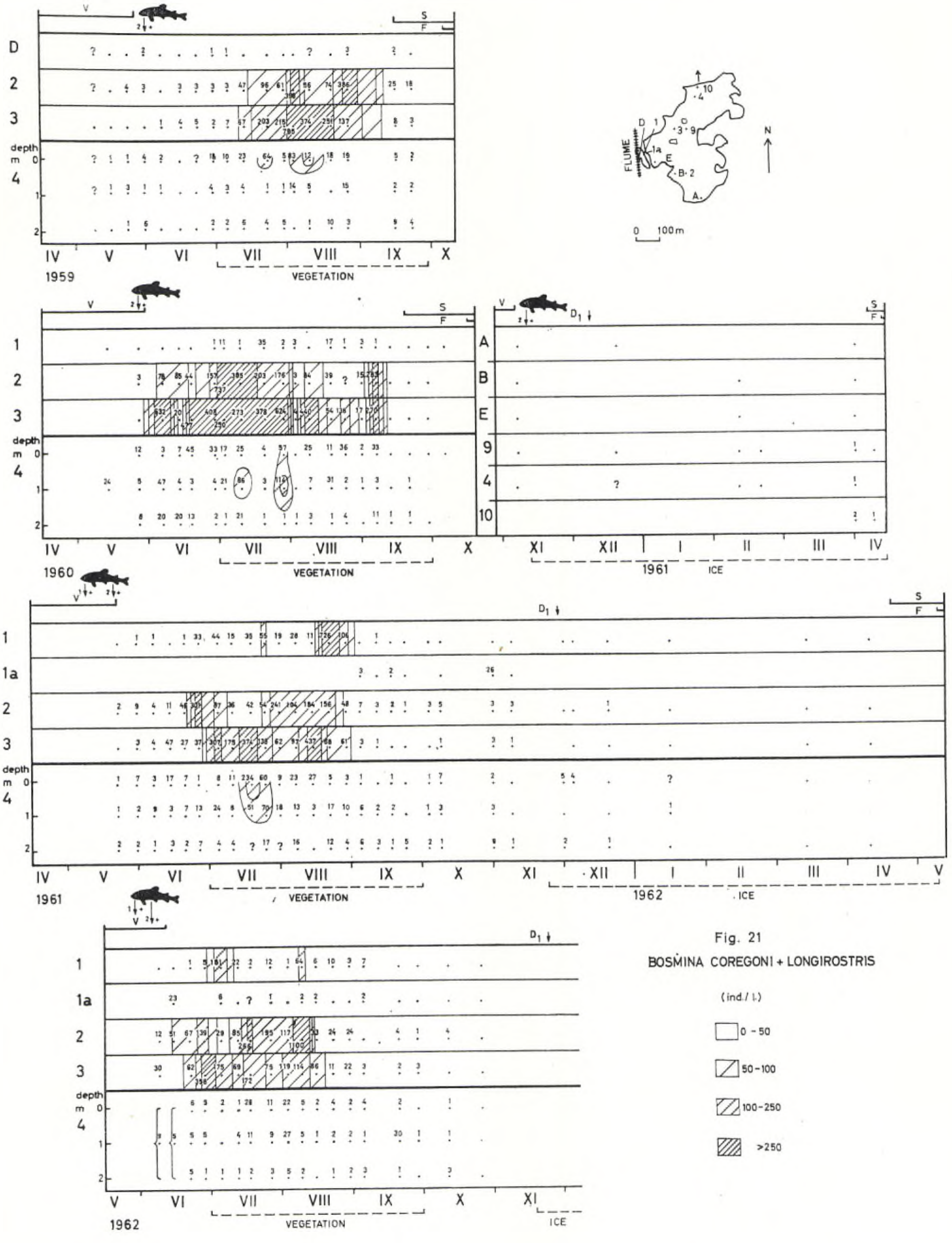
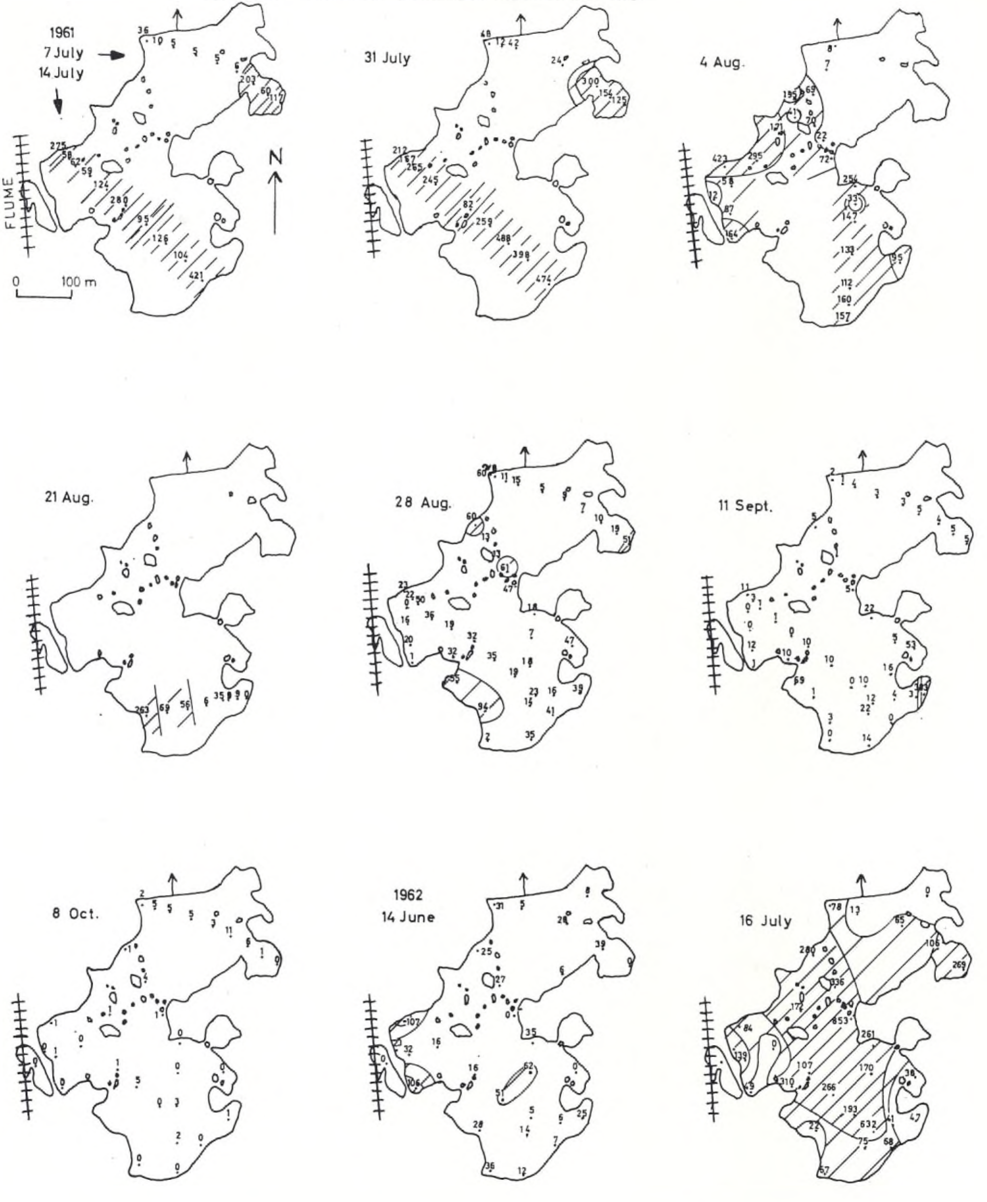


Fig. 21
BOSMINA COREGONI + LONGIROSTRIS

a sample from August 2, 1962. Summarizing the numbers found in the time of high population density it can be said that most samples in areas covered with vegetation contain 100—300 ind./l. and in areas without vegetation 10—30 ind./l.

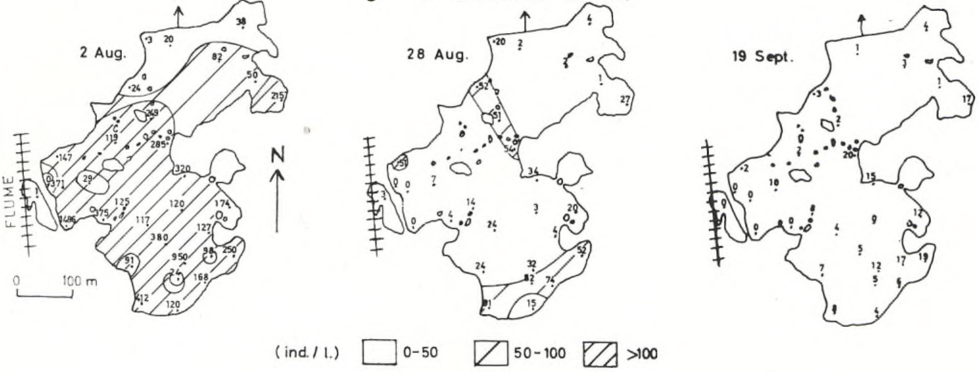
Bosmina as a rule dominates or is one of the dominating species of the

Fig. 22 a BOSMINA COREGONI + LONGIROSTRIS



Cladocera both in lakes and ponds (PEJLER 1961, NAUWERCK 1963). It is sometimes found to be most numerous of the zooplankton (GRIMÅS *et al.* 1954, AXELSON 1961), as is the case in Hyttödammen, when the population densities at the time of the yearly peaks are considered. Without giving any quantitative data, NORDQUIST (1921) in ponds and LÖTMARKER (1964) in lakes found that *Bosmina* dominated the zooplankton. The horizontal distri-

Fig. 22 b BOSMINA cont'd.



bution agrees with that found earlier. Bērziņš (1958) found higher values in the littoral among the vegetation and between the vegetation and the shore (*Bosmina longirostris similis*) than in the pelagial (*Bosmina coregoni longispina*). Axelson (1961) also found higher values of *Bosmina obtusirostris* in the littoral although it was free from vegetation.

Males were found in Hyttödammen in September. In some samples containing more than 100 ind./l. of *B. spp.,* about 5—10 % were males.

Ophryoxus gracilis was present very rarely from July to September in samples taken in the vegetation.

Eurycercus lamellatus occurred very rarely in August and September in samples taken in the vegetation. Because it is benthic, the occurrence of *E. lamellatus* is not properly represented in this investigation. This is confirmed by the observation on fish stomachs, where *E. lamellatus* was frequent.

Camptocercus lilljeborgi was present from July to September at a concentration of 1—4 ind./l. in about 10 % of the samples. It was found more often within the vegetation than outside.

Acroperus harpae was found, though rarely, from June to October. Outside the vegetation it was only found close to the bottom at site 4. One male was observed in the middle of September.

Rhynchotalona rostrata occurred, though rarely, from July to September, both outside and within the vegetation.

Graptoleberis testudinaria was found from July to September, with a more frequent appearance in August. It is almost exclusively found close to the bottom at site 4.

Alonella was present from July to October in about 10 % of the samples, both outside and within the vegetation.

Pleuroxus trigonellus occurred very rarely in August and September, but only among the vegetation. One male was observed in the middle of September.

Chydorus sphaericus was the most common of the *Chydoridae*. It was found from May to October outside and within the vegetation. It is not considered as a planktic species but is often found among zooplankton even in lakes (NAUWERCK 1963, PEJLER 1965). In Hyttödammen it was found at site 4; not only at the bottom but also up at the surface. *C. sphaericus* was found in about 25 % of the samples, as a rule in a concentration of 1—5 ind./l. and a maximum of 20 ind./l. Maximum population density seemed to occur in August.

Polyphemus pediculus (Fig. 23) was almost only found at site 1, where it occurred from June to September. Because of its appearance in swarms, it is impossible to say anything about the maximum size of the population. Observations in the field showed that during the filling of the pond with water, *P. pediculus* rapidly increased in numbers and was found in swarms close to the shore. Later on, competition for food and predation by *Heterocope* (see below) decreased the population density, but there were always some individuals present throughout the summer. The species according to EKMAN (1904), is arctic or subarctic. In the birch-tree region of the subarctic he found it in the littoral of the lakes and in ponds and very small shallow waters. It is also well known from many investigations, e.g. AXELSON (1961) and LÖTMARKER (1964), that it occurs sporadically in the pelagial and that these individuals have been transported by water movements from the littoral where they are common.

If competition and predation did not occur, it is probable that the population of *P. pediculus* would continue to develop in Hyttödammen. With respect to the arctic or subarctic origin of the species, the temperature in the summer in Hyttödammen could influence the development negatively, but the species is widely distributed in Sweden and some parts of Europe (LILLJEBORG 1900) where the temperature is higher. Most probably the disappearance of *P. pediculus* in the pond itself is due to competition for food and predation. However, in the inlet pond where site 1 is situated, the conditions for *P. pediculus* seem to be more favourable. As will be shown later on (p. 260) the zooplankton community at site 1 differs very much from that of the pond itself, in that almost all the animals were *Cladocera*. As *P. pediculus* was the only carnivorus *Cladocera* (NAUMANN 1921) found at site 1, there was thus little competition from the *Copepoda* and the *Rotatoria*. In the pond the *Copepoda,* consisting of littoral forms (the *Cyclopoida*) as well as pelagial (the *Calanoida*), successfully compete with the littoral form *P. pediculus,* in spite of the littoral character of the pond. In addition the numbers are reduced by predation from *Heterocope* (BURCKHARDT 1944), see also p. 243—4. This is different from what can be found in the littoral zone of lakes, where *Bosmina* and *Polyphemus* dominate the zooplankton com-

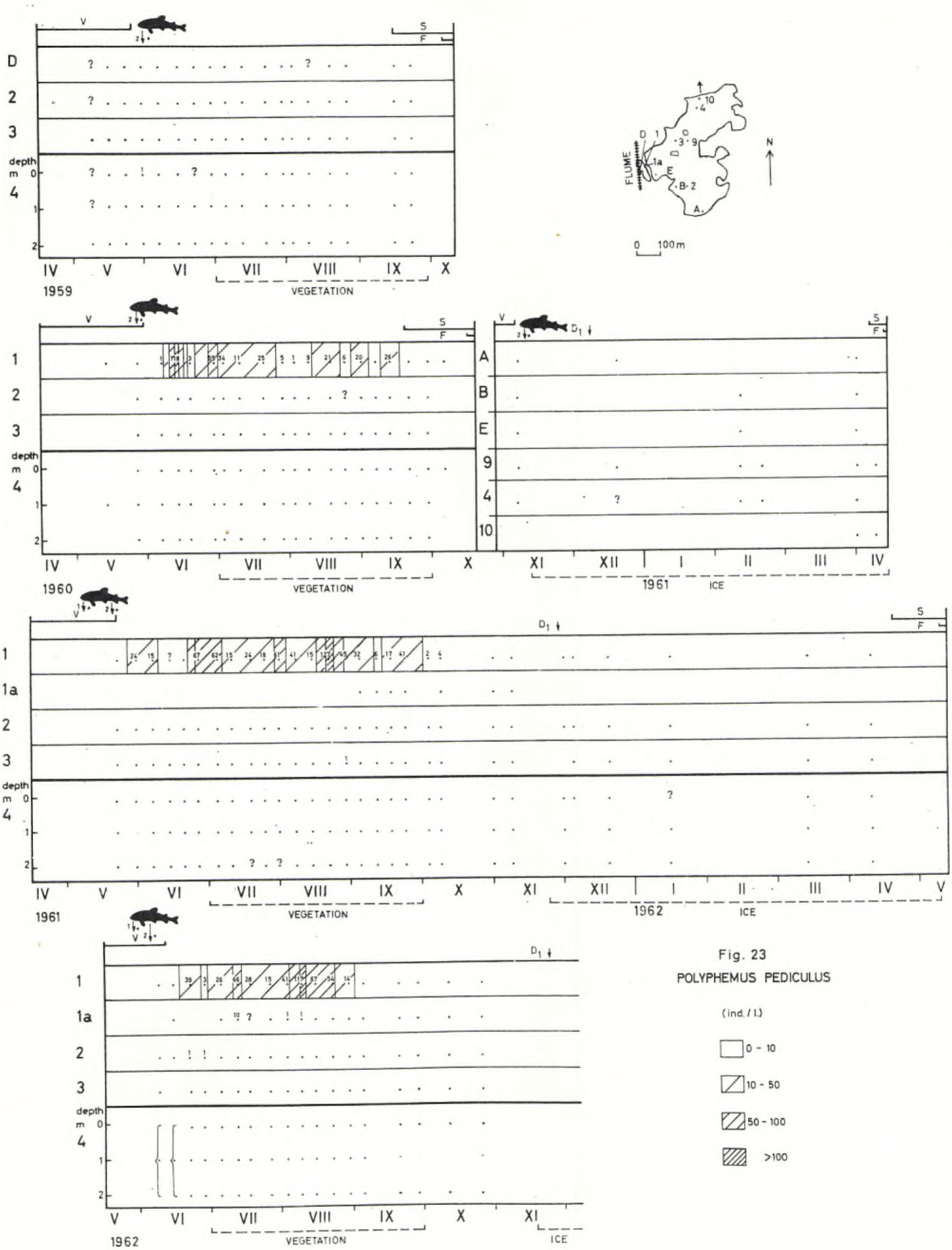


Fig. 23
POLYPHEMUS PEDICULUS

munity. On the other hand the normal picture of a pond probably agrees with that of the littoral in a lake. Thus Hyttödammen must be considered as lying between a strictly littoral pond and a small lake, as far as the composition of the zooplankton is concerned.

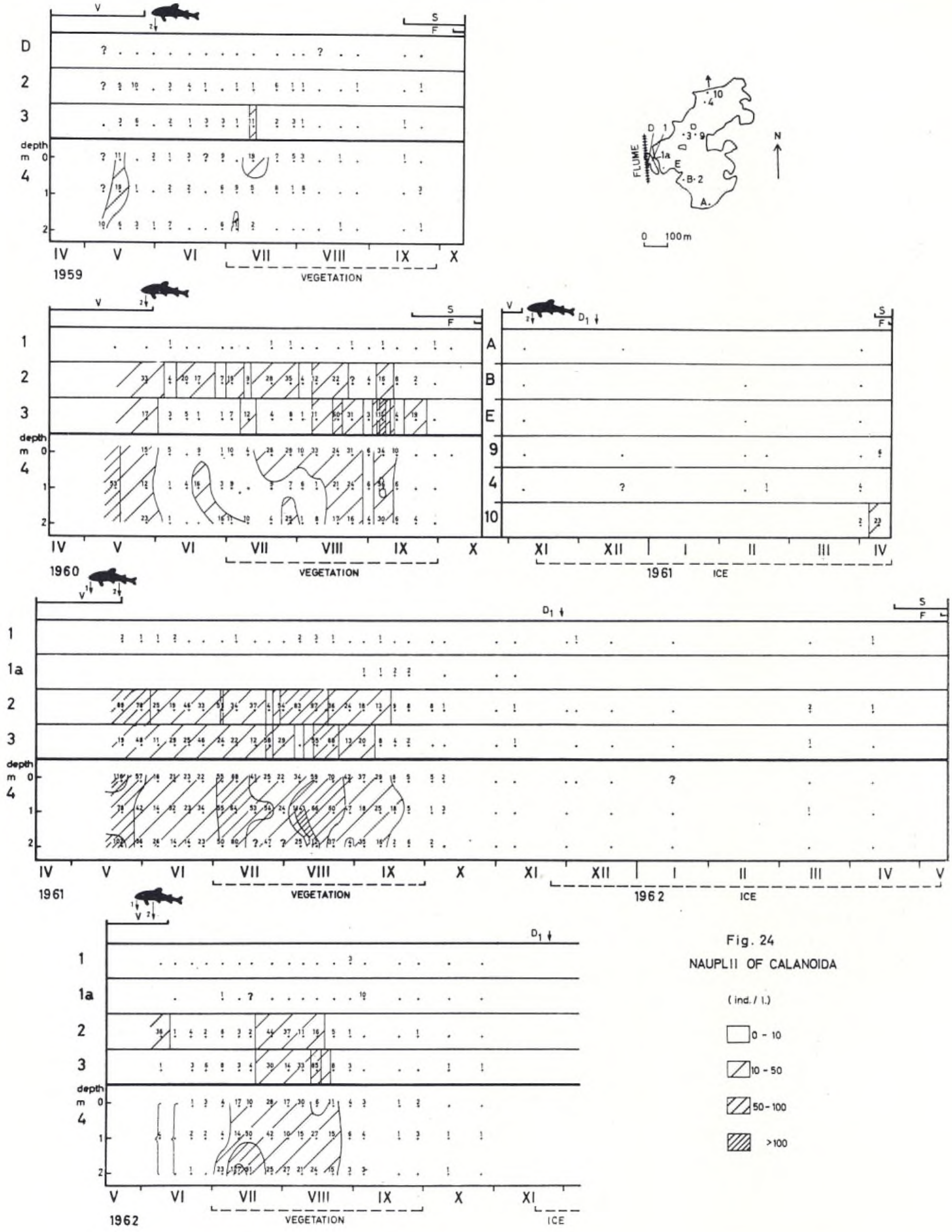


Fig. 24

NAUPLII OF CALANOIDA

(ind. / l.)

☐ 0 - 10

▨ 10 - 50

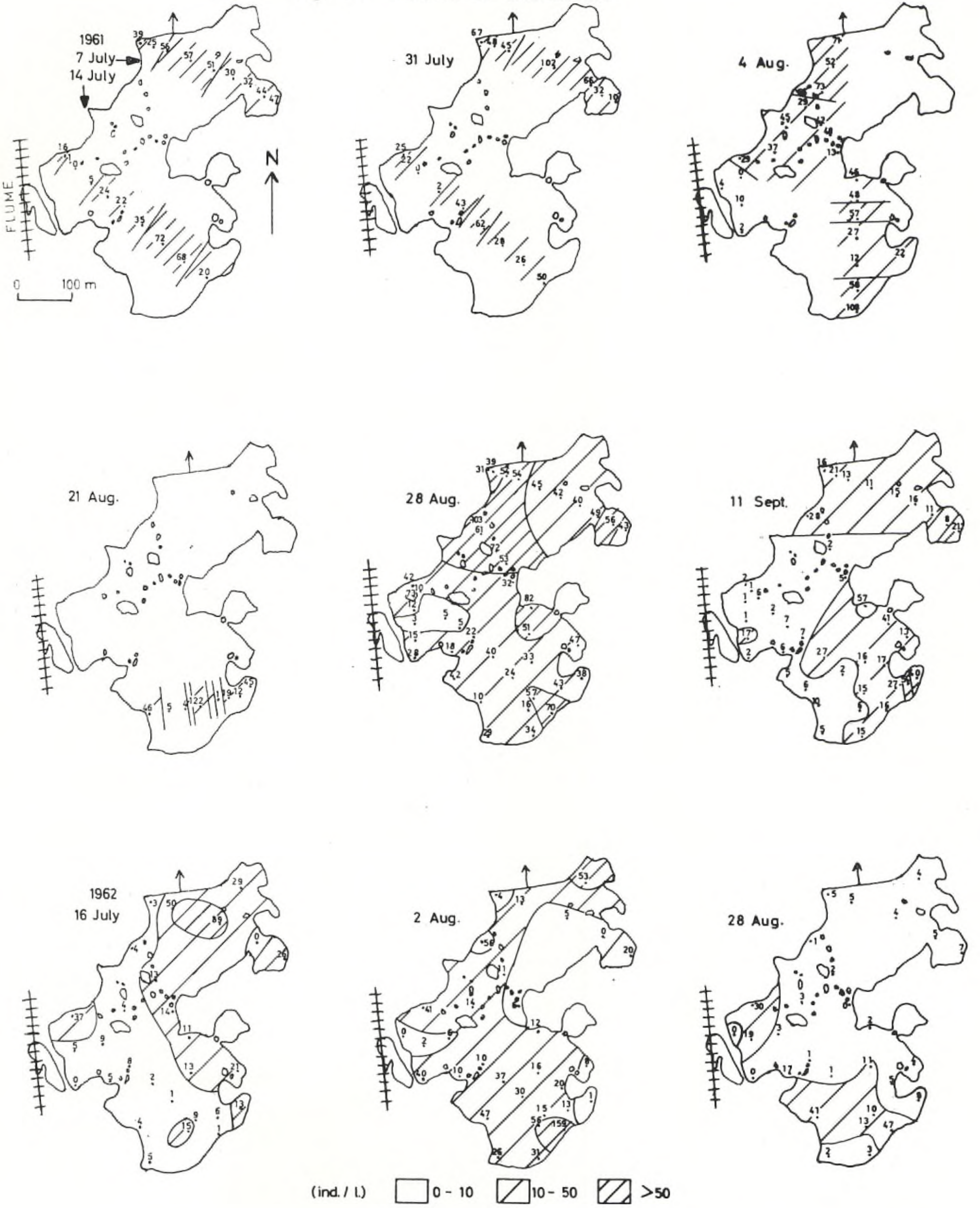
▨ 50 - 100

▨ >100

3. Copepoda

Heterocope appendiculata is the most important of the *Copepoda* for the fish, which eat the adults and to some extent also the copepodids IV—V. The different stages of its development are given on the following Figures: *nauplii* (shown together with those of *Eudiaptomus graciloides*) in Figs. 24

Fig. 25 NAUPLII OF CALANOIDA



and 25; copepodids I—III in Figs. 26 and 27; copepodids IV—V, together with the adults, in Figs. 28 and 29.

From other investigations it appears that *Heterocope appendiculata* never dominates the *Copepoda*. In Hyttödammen it was as common as *Eudiaptomus graciloides,* perhaps even a little more numerous. The *Cyclopoida*

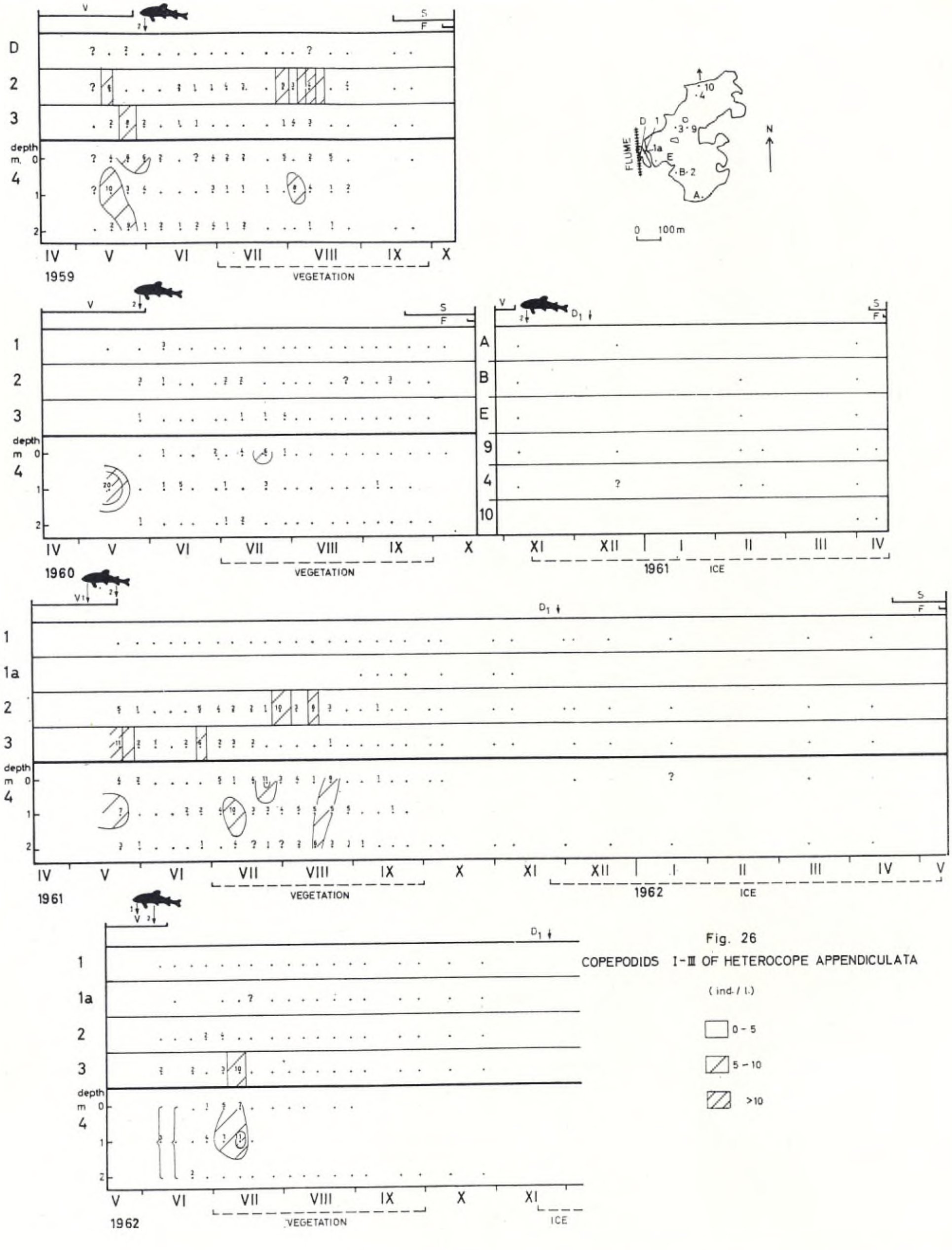


Fig. 26
COPEPODIDS I-III OF HETEROCOPE APPENDICULATA
(ind./l.)

numerically dominated at some times but were never of the same importance as *H. appendiculata*. Measured as volume, *H. appendiculata* was the most important of the *Copepoda*.

There are many problems involved when the annual cycle of *H. appendiculata* is determined from the temporal distribution of the different stages.

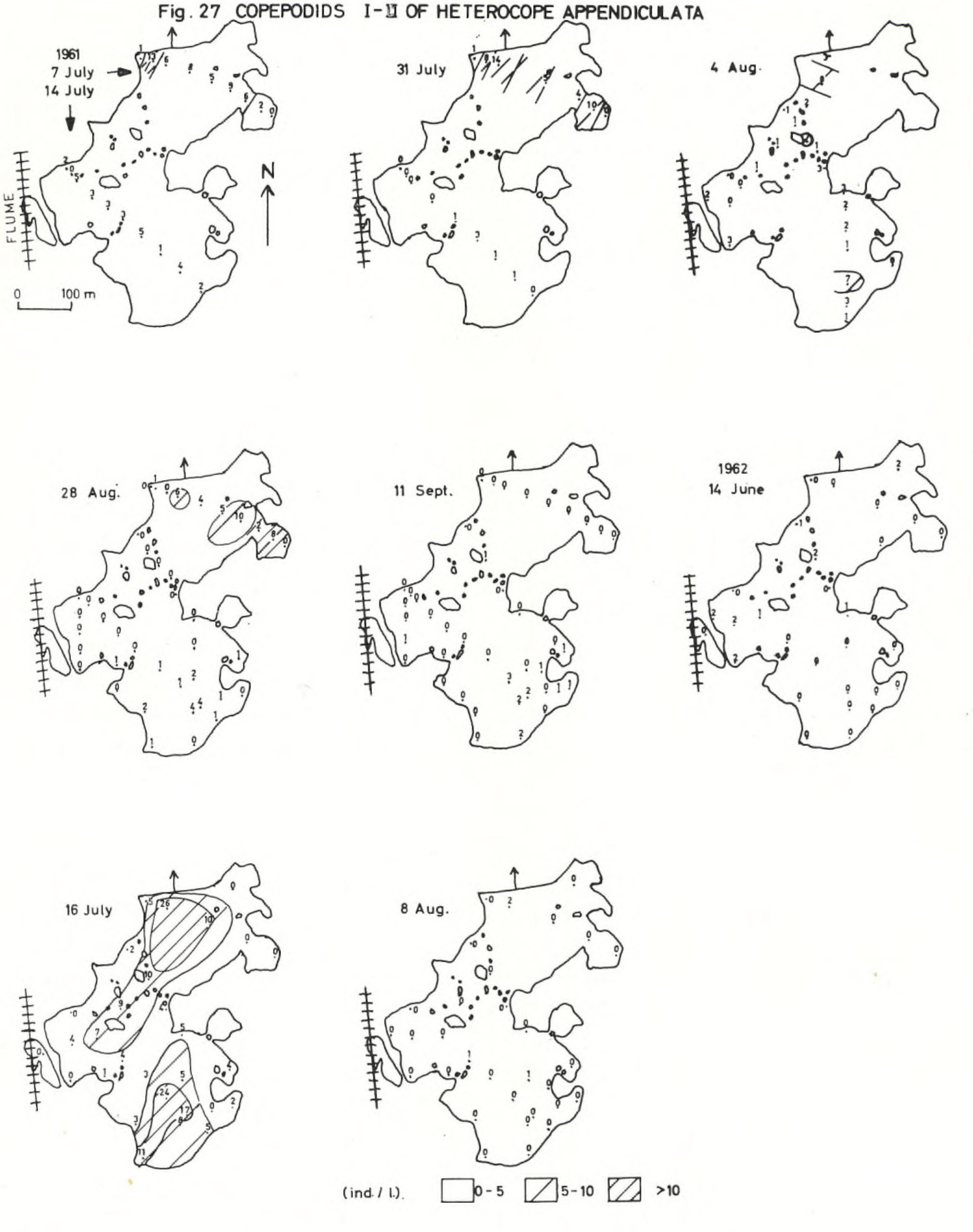


Fig. 27 COPEPODIDS I-III OF HETEROCOPE APPENDICULATA

From the distribution of the *nauplii* little information can be obtained because of the difficulty of distinguishing the *nauplii* of the two calanoid *Copepoda* from each other. However, the proportions of the two species ought to be reflected in the occurrence of the copepodids and the adults. As the oldest stages of *H. appendiculata,* but not *Eudiaptomus graciloides,* are subject to predation, the best information ought to be obtained from the counts of the copepodids I—III as given in Figs. 26 and 30. When comparing them, the material from 1959 is omitted because of the uncertain determinations of the *Copepoda.* Even if the values from the other years are low, making the distinction somewhat uncertain, the values indicate that *E. graciloides* has densest populations in August, with only one yearly peak, and *H. appendiculata* has a maximum in June and July, with perhaps several peaks during the year.

Thus, the high values of *nauplii* in Fig. 24 in May 1960 and 1961 most probably belong to the predominating *H. appendiculata,* while in June *E. graciloides* predominates. Later in the summer, the proportions of the two species are more difficult to determine. Except at site 1 no differences in the occurrence of the *nauplii* at the different sites are to be found in Fig. 24. The horizontal distribution in Fig. 25 does not give any further information about significant differences in the pond. Only the region closest to the inlet of Dalälv water from the inlet pond, where site 1 is situated, shows lower values. The water inflow is so small that the observed irregularity of distribution is not due to any velocity of the water. It is possibly an effect of unknown environmental factors.

As there is no information about the biology of *Heterocope appendiculata,* the following description of the annual cycle of the population of *H. appendiculata* (considered a warm-water form; RYLOV 1935) has to be compared with the results of ELSTER's (1936) careful investigation of the biology of *H. borealis* (considered a cold-water form).

ELSTER found that *H. borealis* in the Bodensee began its cycle in the spring when the eggs hatched to produce *nauplii.* The eggs were laid the previous autumn from August to December. The hatching of the eggs and the development stages of the *nauplii* took place at the very low temperature of the bottom water. In the lake a calculated time of about 60 days was necessary for development to copepodid stage IV, and thirty days after becoming adult the individuals were sexually mature and began to reproduce.

As the first copepodids IV in Hyttödammen appeared in 1961 30 days after the beginning of the filling of the pond with water (and 4 days after its completion) the development was more rapid than that in the Bodensee. The time of development for the eggs has long been known to depend upon the temperature, although the ideas of ELSTER (1936) were ignored and not applied to other species of zooplankton until ELSTER and his school started new investigations of other *Copepoda* and also applied the ideas to the *nauplii* and the copepodids (NAUWERCK 1963, and literature cited by him). The investigations have also been widened to include the rotifers (EDMONDSON 1960, AMRÉN 1964). Thus the development of the different stages of *H. appendiculata* is favoured by the temperature.

Another factor of importance observed by ELSTER (1936) determining that all the eggs hatched within a very short period of time, was exposure of the eggs at some time to a higher temperature (14—16°C) than that of the lake (4—6°C). ELSTER set this "warm" period at 4 weeks and he did not perform further experiments to show whether the duration of the period was of significance. Perhaps a short-time exposure would also function as an alarm clock to the eggs. Hyttödammen is drained for at least one week in the spring and the bottom with the eggs is exposed to air temperature, which at Gävle reached a maximum on the warmest day of April 1959, 1960, 1961 and 1962 of 19.8, 15.8, 19.3 and 14.0°C, respectively. The mean of the maximum temperatures for April was 9.7 and 7.8°C in 1961 and 1962 respectively. (Data obtained from SMHI Yearbooks 1959—1962.) The warm daytime temperatures perhaps in combination with the cold temperatures at night, seem to have sufficed as an alarm clock, to judge from the rapid growth of the population and from the appearance of the adults very soon after the filling of the pond. For the fish this is very important, as the oldest stages of *H. appendiculata* to a large extent serve as food for the fish from the time of their planting.

Through this warm-period exposure observed by ELSTER in the laboratory all the eggs were hatched within a short period, or at any rate within a much shorter period than in nature. That means that in Hyttödammen the copepodids I—III, occurring in July and August (see Figs. 26 and 27), probably develop from eggs laid in the same summer, and that at least two generations are to be found in Hyttödammen. ELSTER found that *H. borealis* in Bodensee was monocyclic.

The horizontal distribution of the copepodids I—III in Fig. 27 presents the same pattern as is described on p. 240 for the *nauplii.*

The copepodids IV—V, together with the adults of *H. appendiculata,* were found from May to October (Fig. 28). ALM (1916) found the same temporal distribution in Hjälmaren (central Sweden) as in Hyttödammen.

The horizontal distribution in Fig. 29 does not show any significant differences. The observation that the *nauplii* and the copepodids I—III avoided the surroundings closest to the inlet of Dalälv water is not true for the older stages. It is also quite obvious that the pelagic species *H. appendiculata* is also to be found among vegetation.

Information about *H. appendiculata* is sparse. The species was described by SARS (1863), who found it to be more common in the larger of the lakes investigated by him in Norway. It was common in the southern parts of Norway but was replaced by *H. robusta,* now called *H. saliens,* towards the north. FREIDENFELT (1913) observed in his investigations of *Daphnia* in south Sweden that *H. appendiculata* made diurnal vertical migrations, but gave no more information. LÖTMARKER (1964) observed *H. appendiculata, H. borealis,* and *H. saliens* in his investigation of 13 lakes in northern Sweden. However, only one of the species occurred in every lake, and *H. appendiculata* was

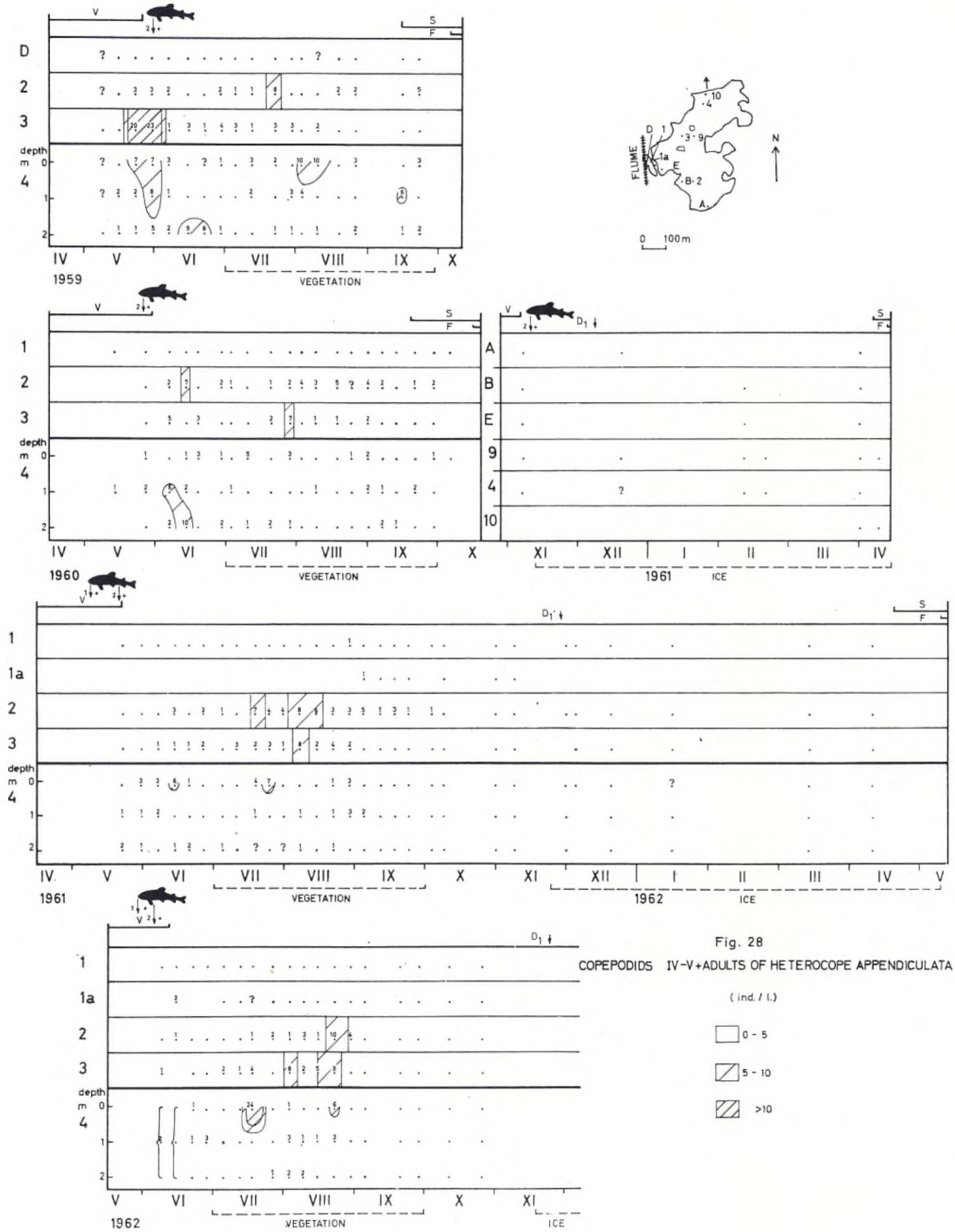


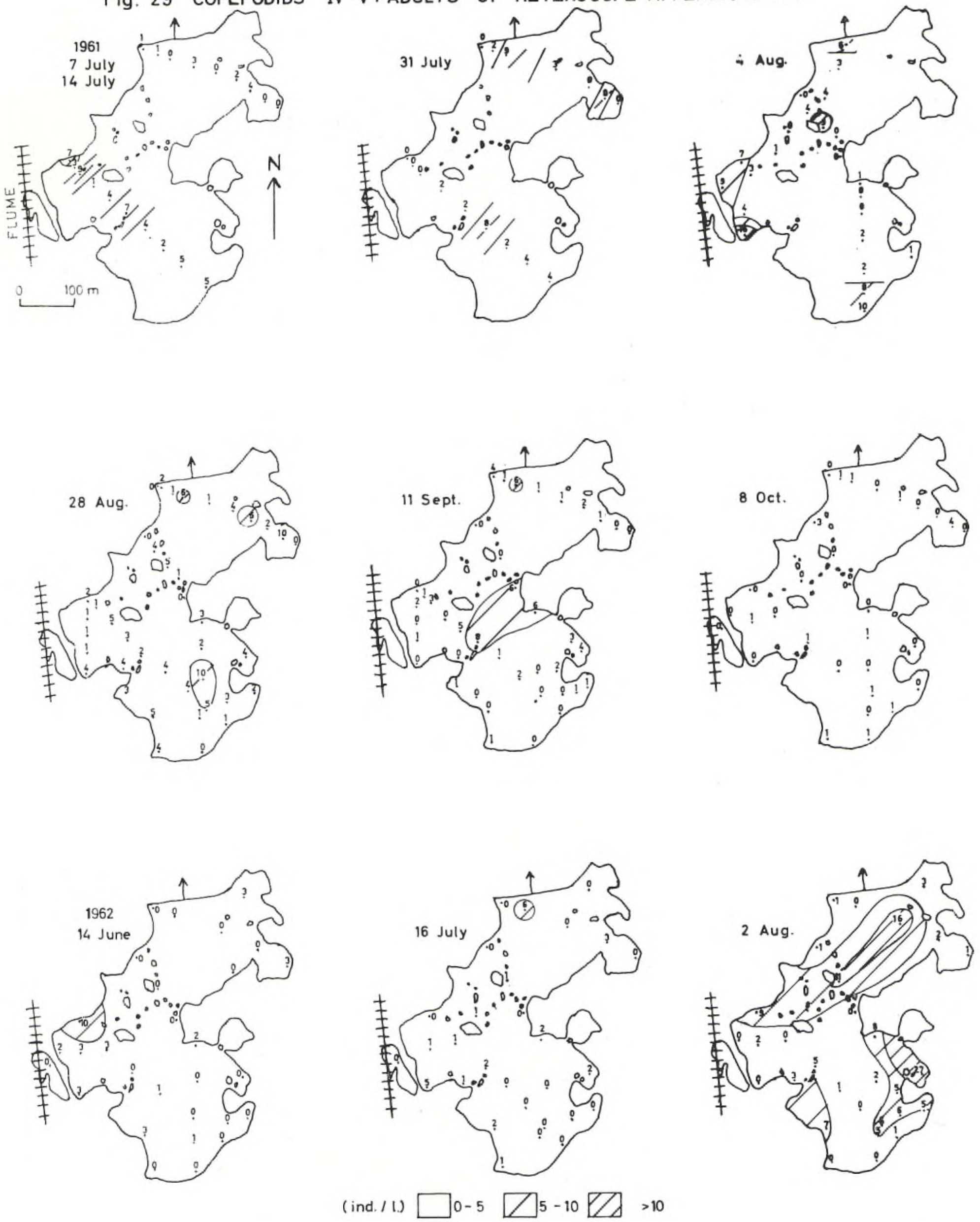
Fig. 28

COPEPODIDS IV–V + ADULTS OF HETEROCOPE APPENDICULATA

(ind. / l.)

to be found in 4 of the lakes, namely those situated in the conifer region. Maximum population density was to be found between 0—5 m. The time of development was much shorter for *Heterocope* than for all the other *Copepoda*. PEJLER (1965) in his large regional investigation of the distribution of the zooplankton in central Sweden found that *H. appendiculata* avoided

Fig. 29 COPEPODIDS IV-V + ADULTS OF HETEROCOPE APPENDICULATA



shallow lakes and was restricted to oligotrophic lakes. An interesting observation about the food of *Heterocope* was given by Burckhardt (1944). He found that in small lakes the predation by *Heterocope* upon the *Rotatoria* and *Cladocera* caused an almost total depletion of these forms. In addition the effect of predation most probably varies with different species in different environments. In all likelihood because of this, *Bosmina* in Hyttödammen appears in large numbers in spite of its role as a probable prey for *Heterocope*. In contrast, *Polyphemus pediculus* is found in low numbers.

Biometrical data were given by RYLOV (1935). The females were 2.0—2.2 mm in length and the males 1.8—2.0 mm. However, in Hyttödammen *H. appendiculata* is longer than that. The longest individual measured, taken on May 26, 1960, was 3.4 mm. The measurements were made on fixed material and were intended for calculations of the volume. I was not then aware of the lack of biometric information in the literature on the different stages of development and only divided the material into the groups I needed. From the beginning of May to the end of August about 100 individuals were measured every fourteen days. From these measurements it seems as if the first generation of the year is much larger than the following:

The number of *Heterocope appendiculata* found in the longest length-classes.

1960 Total length mm	May 26	June 6	June 18
2.8—2.89	13	—	1
2.9—2.99	2	—	—
3.0—3.09	3	—	—
3.1—3.19	—	—	—
3.2—3.29	2	1	—
3.3—3.4	3	—	—

This decrease in the number of long individuals is most probably due to normal mortality, rather than mortality caused by predation of the fish. That the following generation is shorter in length than the first is possibly a consequence of a better supply of food for the first generation (see p. 267) or of temperature. MARGALEF (1955) observed that individuals of the same species are larger in a cold than in a warm environment. In Hyttödammen the temperature is lower during the time of development of the first generation than of the later ones.

Eudiaptomus graciloides comes next in importance of the *Copepoda* after *Heterocope appendiculata* in Hyttödammen. The different stages of its development are given in the following Figures: *nauplii* (shown together with those of *Heterocope appendiculata* and described on p. 240) in Figs. 24 and 25; copepodids I—III in Figs. 30—31; copepodids IV—V, together with the adults, in Figs. 32 and 33.

The earlier stages of the cycle of the population in May probably have shorter times of development than are usual in nature, as was discussed on p. 240. To judge from the appearance of the copepodids I—III, the first *nauplii* in the spring overwhelmingly belong to *Heterocope* and not to *Eudiap-*

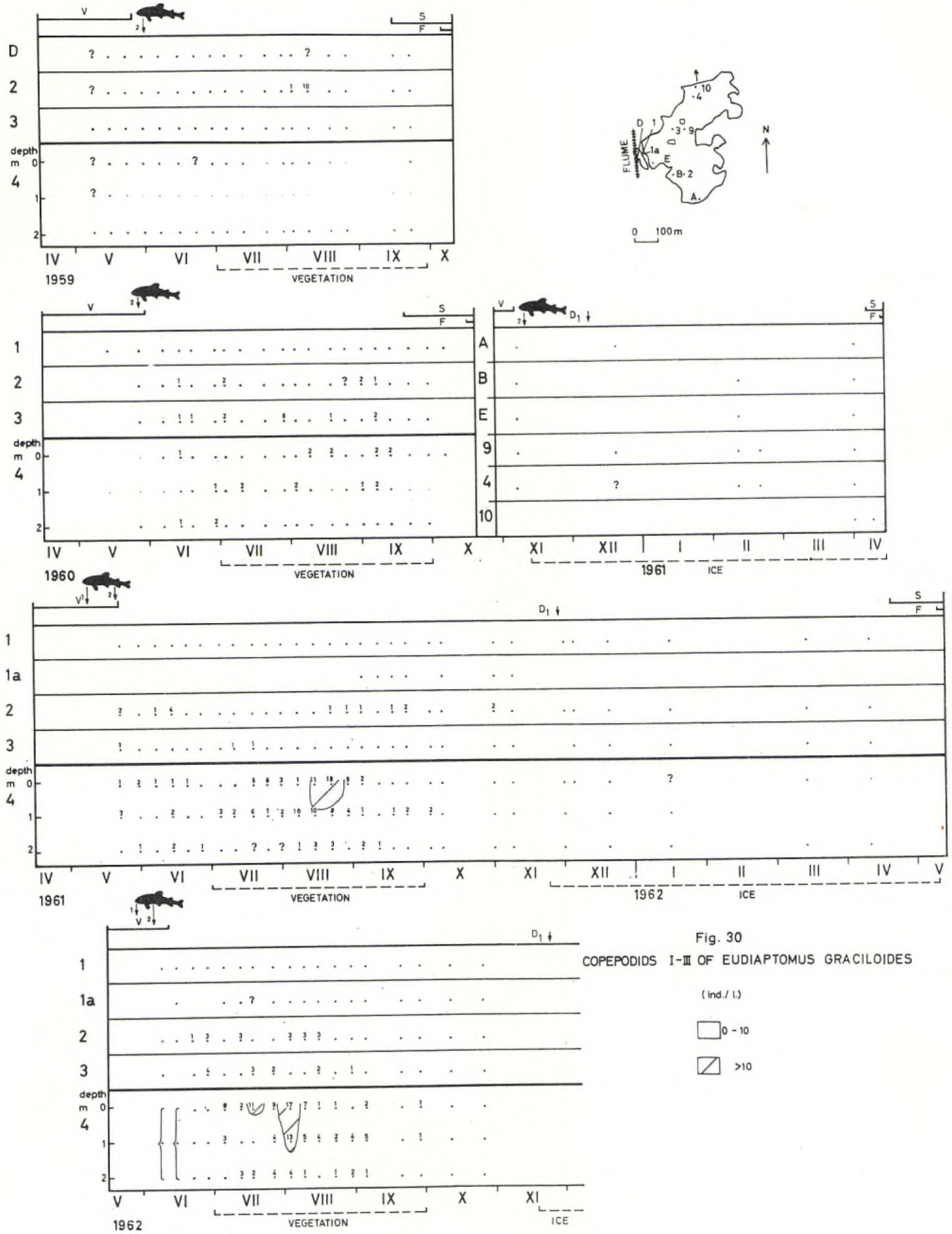


Fig. 30

COPEPODIDS I-III OF EUDIAPTOMUS GRACILOIDES

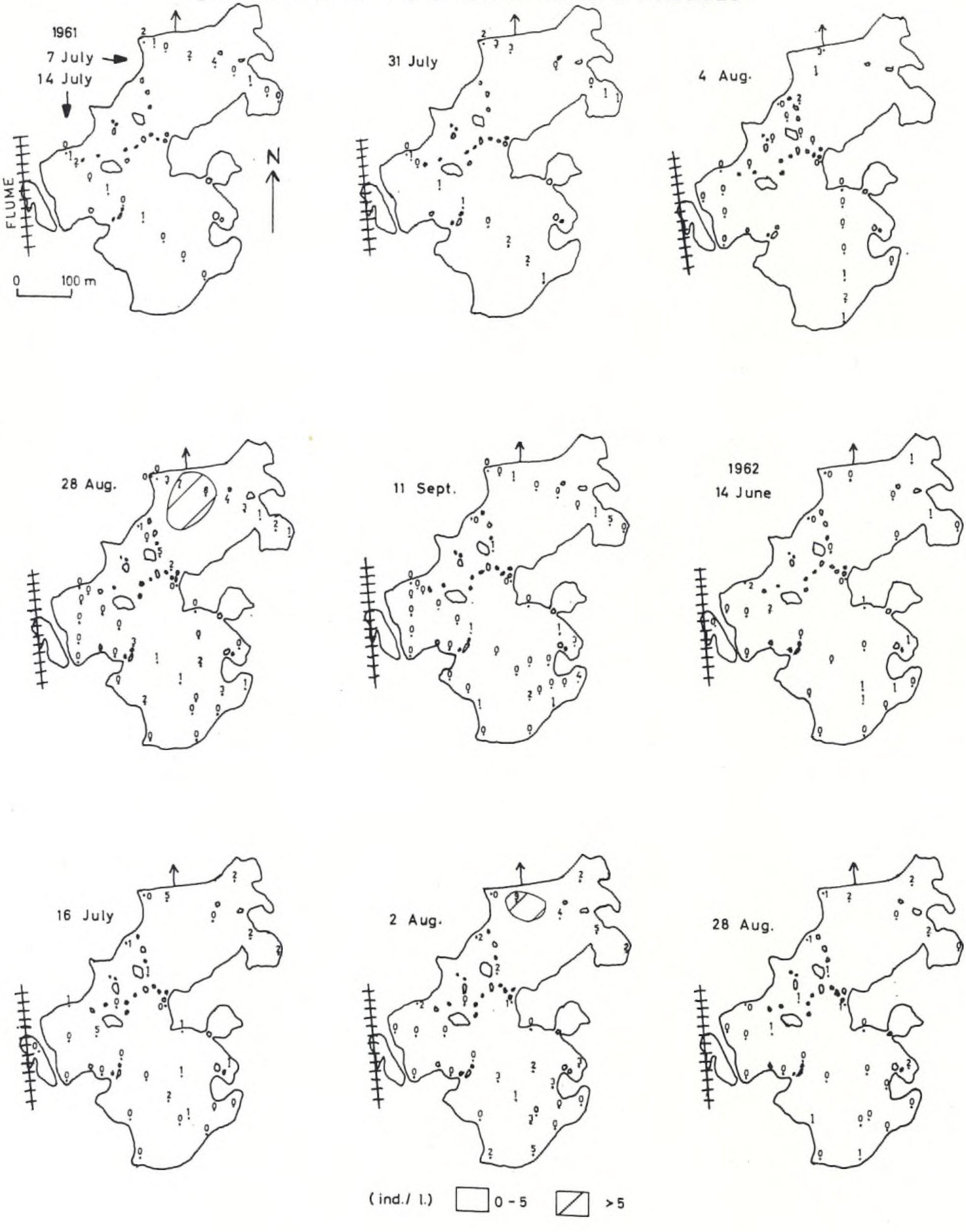
(ind./l.)

☐ 0 - 10

▨ >10

tomus. Another possibility is that a large population of *nauplii* of *Eudiaptomus* was reduced through competition for food (see Fig. 30). Maximum population density seemed to occur at the end of July and August. The numbers of ind./l. were somewhat higher at site 4 than at the other sites. The horizontal distribution in Fig. 31 shows this also, but the difference is less

Fig. 31 COPEPODIDS I-III OF EUDIAPTOMUS GRACILOIDES



significant. The vertical distribution at site 4 showed higher values at the surface and 1 m than at the bottom.

According to Fig. 32 the copepodids IV—V and the adults were most common in August. The horizontal distribution in Fig. 33 shows, as was observed for the *nauplii* and the copepodids I—III of *Heterocope appendi-*

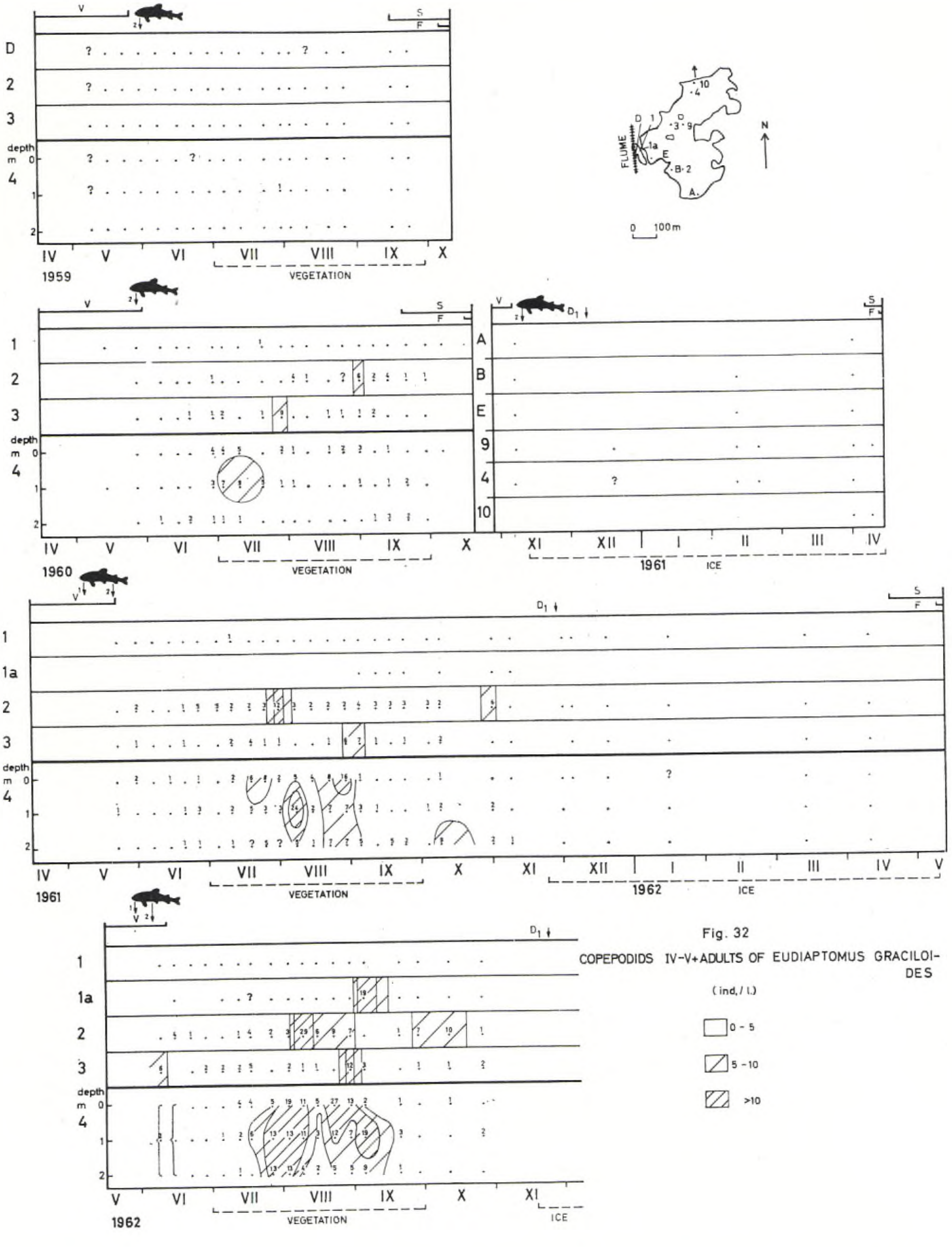


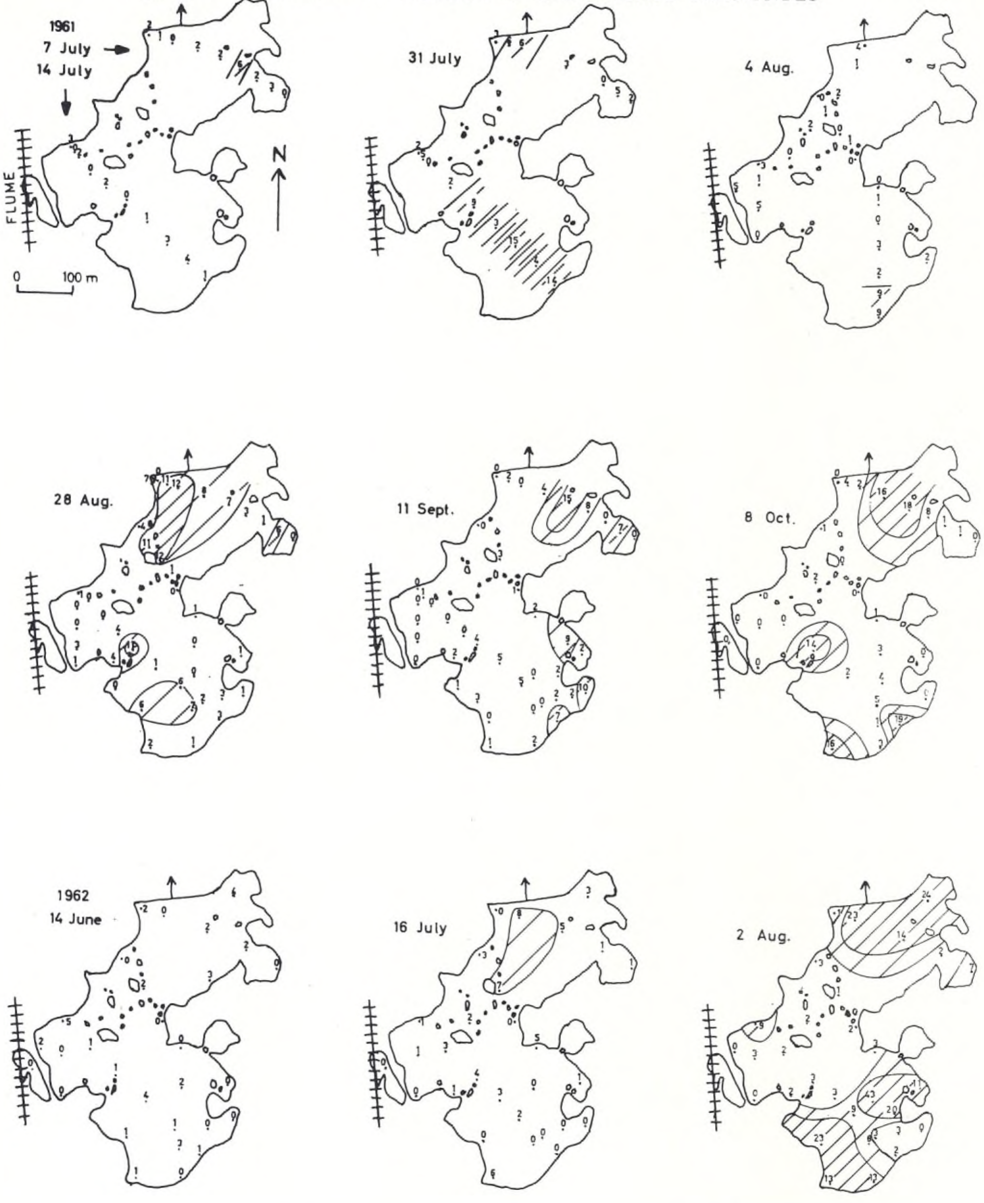
Fig. 32

COPEPODIDS IV-V+ADULTS OF EUDIAPTOMUS GRACILOIDES

culata, that lower numbers of ind./l. are found in the part of the pond where the Dalälv water enters.

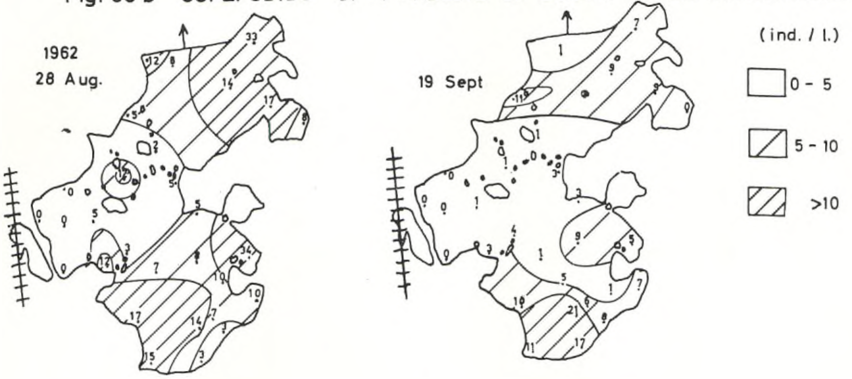
Eudiaptomus graciloides is common in plankton from lakes and ponds. **Ekman** (1964) has studied the cycle of the species in lakes and "wintergeschlossene Seichtgewässer" in northern Sweden, where predation did not

Fig. 33 a COPEPODIDS IV-V+ADULTS OF EUDIAPTOMUS GRACILOIDES



influence the population in any way. He found that *E. graciloides* in the two types of environments differed somewhat as to the time of occurrence of the different stages. In the lakes the adults (expressed as a percentage of the different stages) occurred at a maximum level from October to December and many of the individuals from this maximum were found under the ice in March-April. In the small shallow waters the adults begin to appear

Fig. 33 b COPEPODIDS IV -V + ADULTS OF EUDIAPTOMUS GRACILOIDES cont'd.



in the middle of July and are at a maximum level from September to November. They die in January-February. In both types of environment, EKMAN found only one generation each year. In Hyttödammen it is impossible to say whether more than one generation is to be found. The temperature in Hyttödammen is high during a longer time than in the small waters studied by EKMAN in the arctic and subarctic region, making it possible for more than one generation to develop. However, the conditions are not similar to those in Lake Erken, lying in about the same climate as Hyttödammen, where NAUWERCK (1963) found *E. graciloides* to be by far the most important of the *Copepoda,* producing several generations in the year.

The *Cyclopodia* of the *Copepoda* have been determined by Dr. U. EINSLE to contain the following species: *Macrocyclops albidus, Eucyclops serrulatus, Cyclops, Megacyclops viridis, Mesocyclops leuckarti.*

The different stages of the *Cyclopoida* are given in the following Figures: *nauplii* in Figs. 34 and 35; copepodids I—III in Figs. 36 and 37; copepodids IV—V, together with the adults, in Figs. 38 and 39.

As shown in Fig. 34, the *nauplii* were found almost throughout the year. The number of ind./l. from the end of September and throughout the whole winter are very low. The numbers at the different sites do not differ significantly and there is a large variation to be found between years. In 1959 and 1962 the *nauplii* were by far more numerous than in 1960—61. No pronounced time of maximum can be determined. The horizontal distribution as presented in Fig. 35 shows that there is a tendency towards lower values close to the inlet of Dalälv water in the pond.

The copepodids I—III, shown in Fig. 36, were to be found at about the same time, at the same places, and at the same concentrations as the *nauplii.* However, the mortality in the large population of *nauplii* 1959 and 1962 was high and the copepodids in those years were about as numerous as in 1960—61. The horizontal distribution in Fig. 37 did not show any significant differences between different parts of the pond as the *nauplii* tended to do.

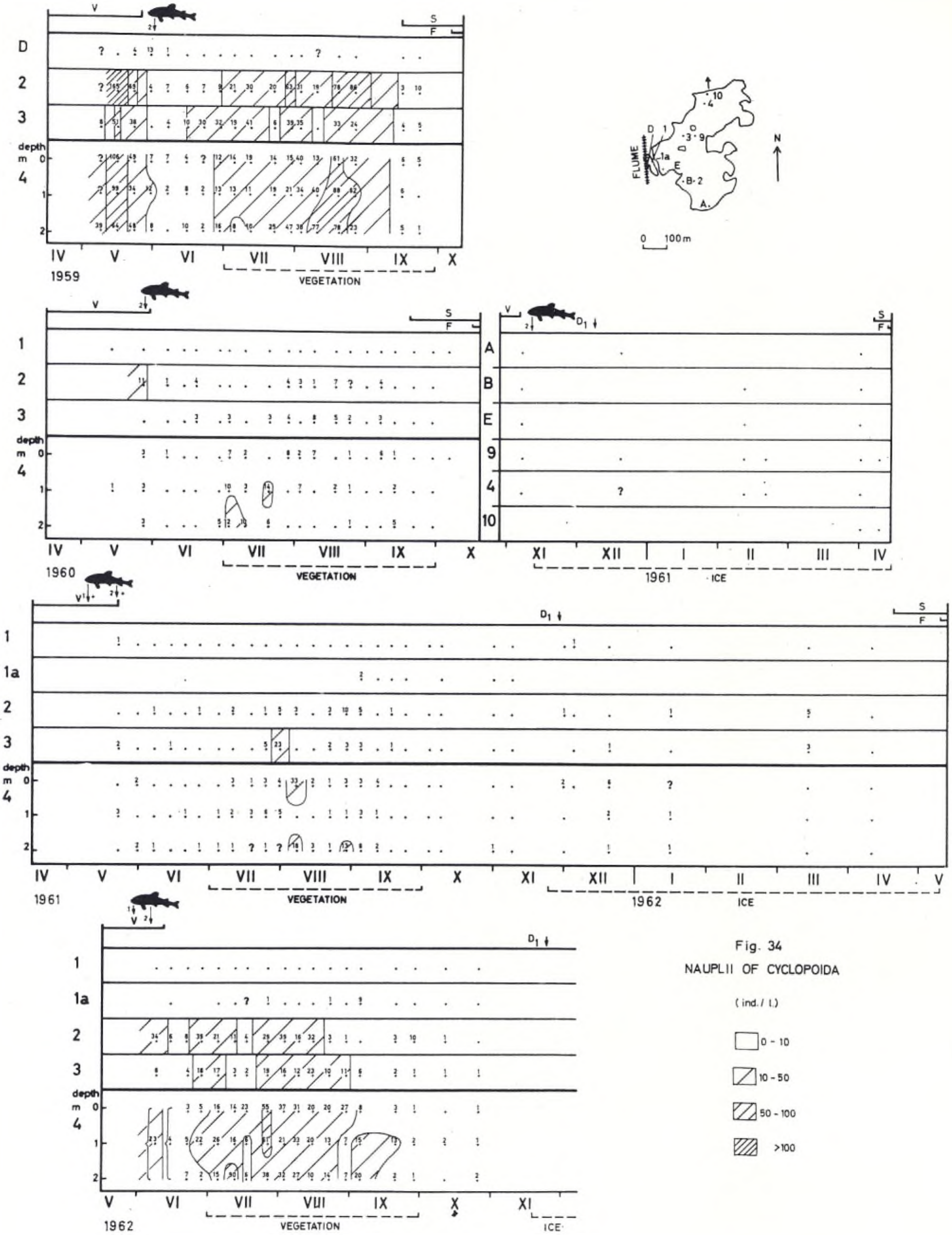
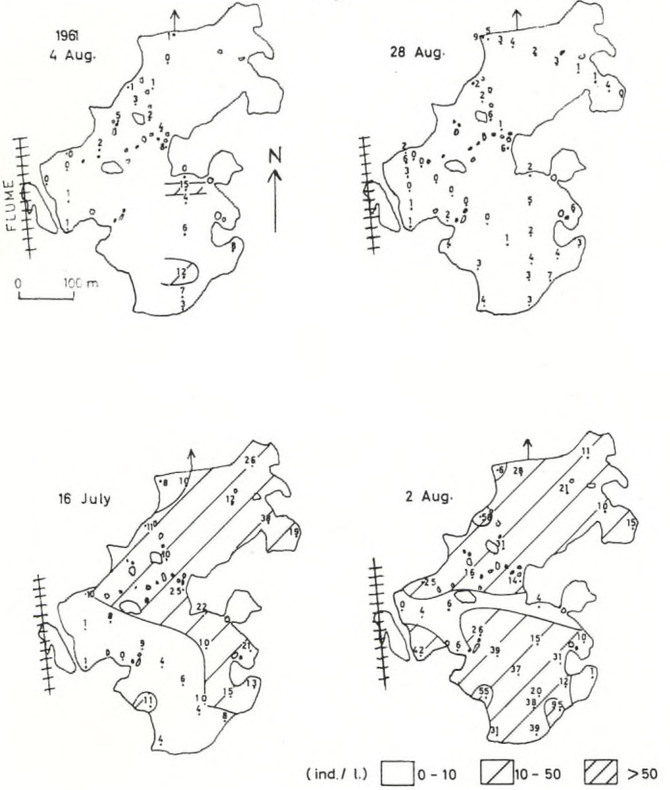


Fig. 34
NAUPLII OF CYCLOPOIDA

The copepodids IV—V and the adults, according to Fig. 38, were found in low numbers throughout the summer, with a maximum at the end of May, indicating the same rapid development as is described on p. 240. They were equally numerous at the different sites. The horizontal distribution as shown in Fig. 39 gave no information about any horizontal differences. On

Fig. 35 NAUPLII OF CYCLOPOIDA



June 14, 1962, when high values were found, low values were observed in the part of the pond where later no vegetation grew up. Even though the vegetation had not yet grown up, the shallower areas seem to be preferred.

4. Standing crop of zooplankton

The standing crop of zooplankton, shown in Fig. 40, was calculated as mm³/l. as a rule. The highest values were found in July and August. The highest value ever found, 73.4, was on August 21, 1961, at site 1. The values varied from week to week at every site, apparently depending partly on the aggregation of the different species in swarms (cf. p. 208) and partly on the successions of species and generations (cf. p. 260).

From Fig. 40 it can also be seen that the summer values at site 4 are lower than at sites 1, 2 and 3. At site 4 the vertical distribution showed no stable long-term stratification. The values from 1959 were taken at site 2 and 3 at a lower level than in the other years.

The horizontal distribution of the zooplankton expressed as standing crop in mm³/l. is shown in Fig. 41. From the Figure it can be seen that the lower

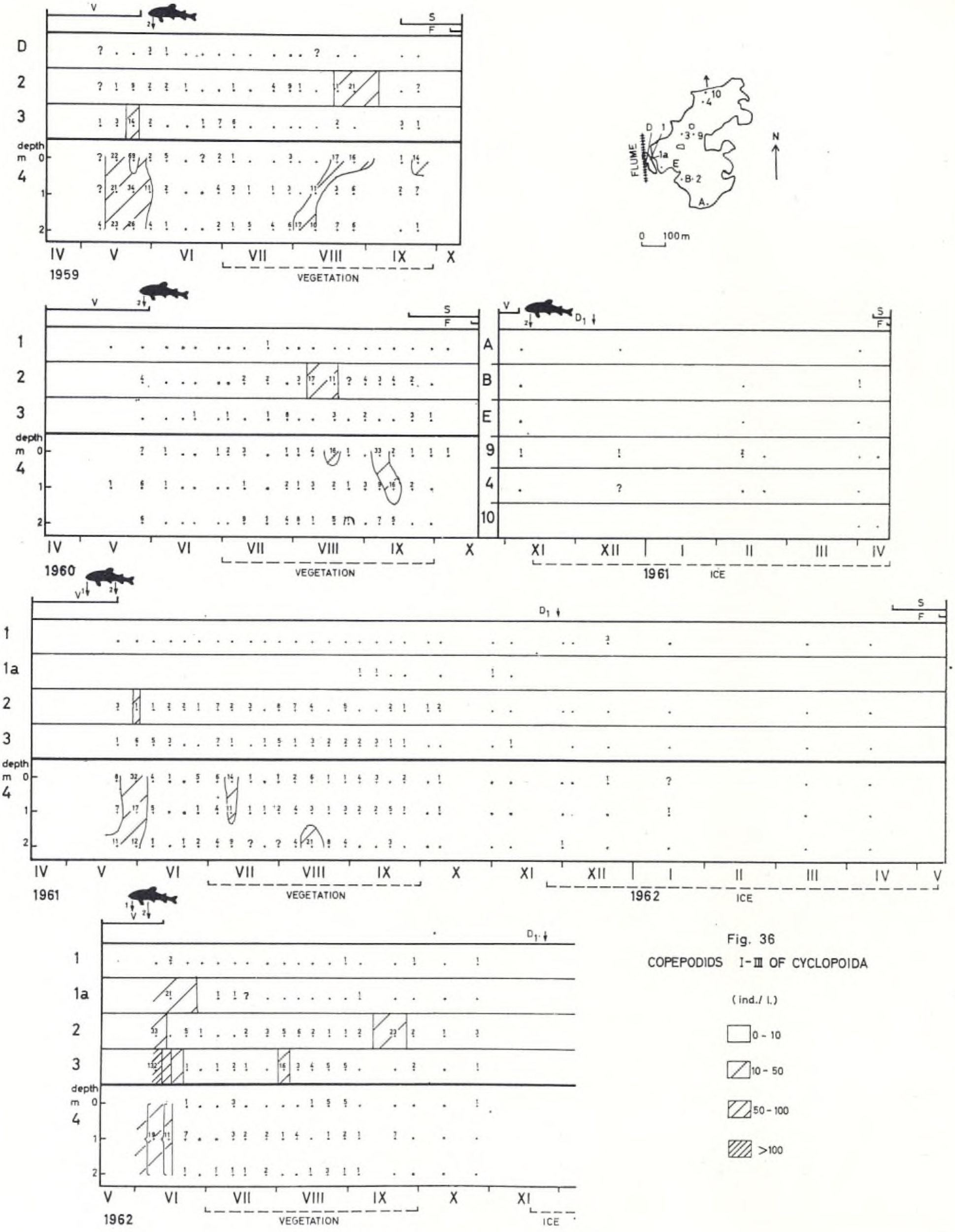
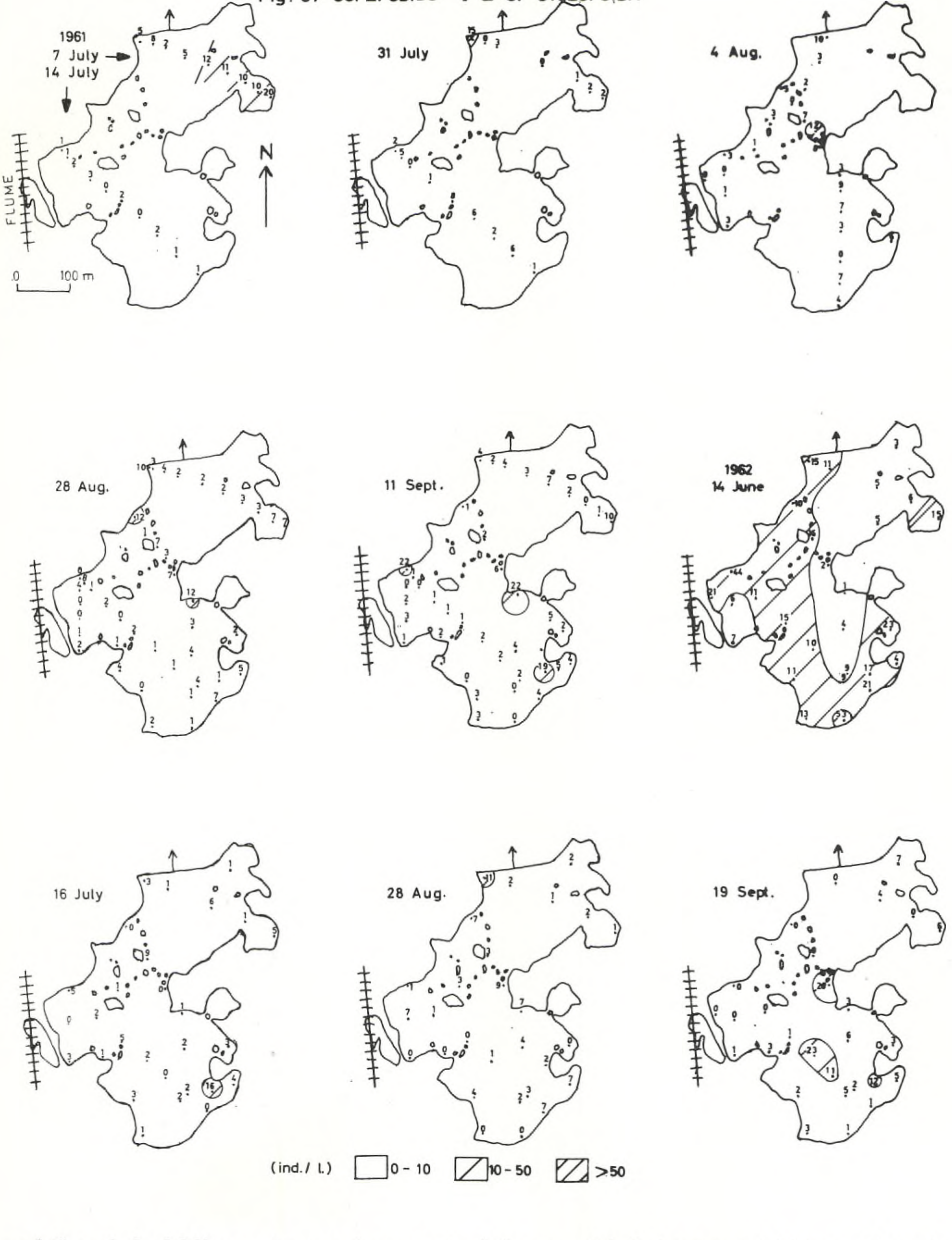


Fig. 36
COPEPODIDS I-III OF CYCLOPOIDA

result from site 4 noted above does not hold for all parts of the pond that are free of vegetation. This is especially clear from the results of July 16 and August 2, 1962, when the biomass was high in the whole pond. The values obtained in the winter (December 4, 1961, and January 15, 1962) were about the same in the whole pond irrespective of the different depths at the sites and

Fig. 37 COPEPODIDS I-III OF CYCLOPOIDA



of the air bubbling going on in a part of the pond (cf. ARNEMO 1964, p. 10 and Fig. 7 c). In the autumn there was a tendency for higher values in the south-eastern parts of the pond than in the vicinity of the inlet of Dalälv water. These two areas have about the same quantities of vegetation, but the water is of different chemical composition (ARNEMO 1964, pp. 83—85), and the

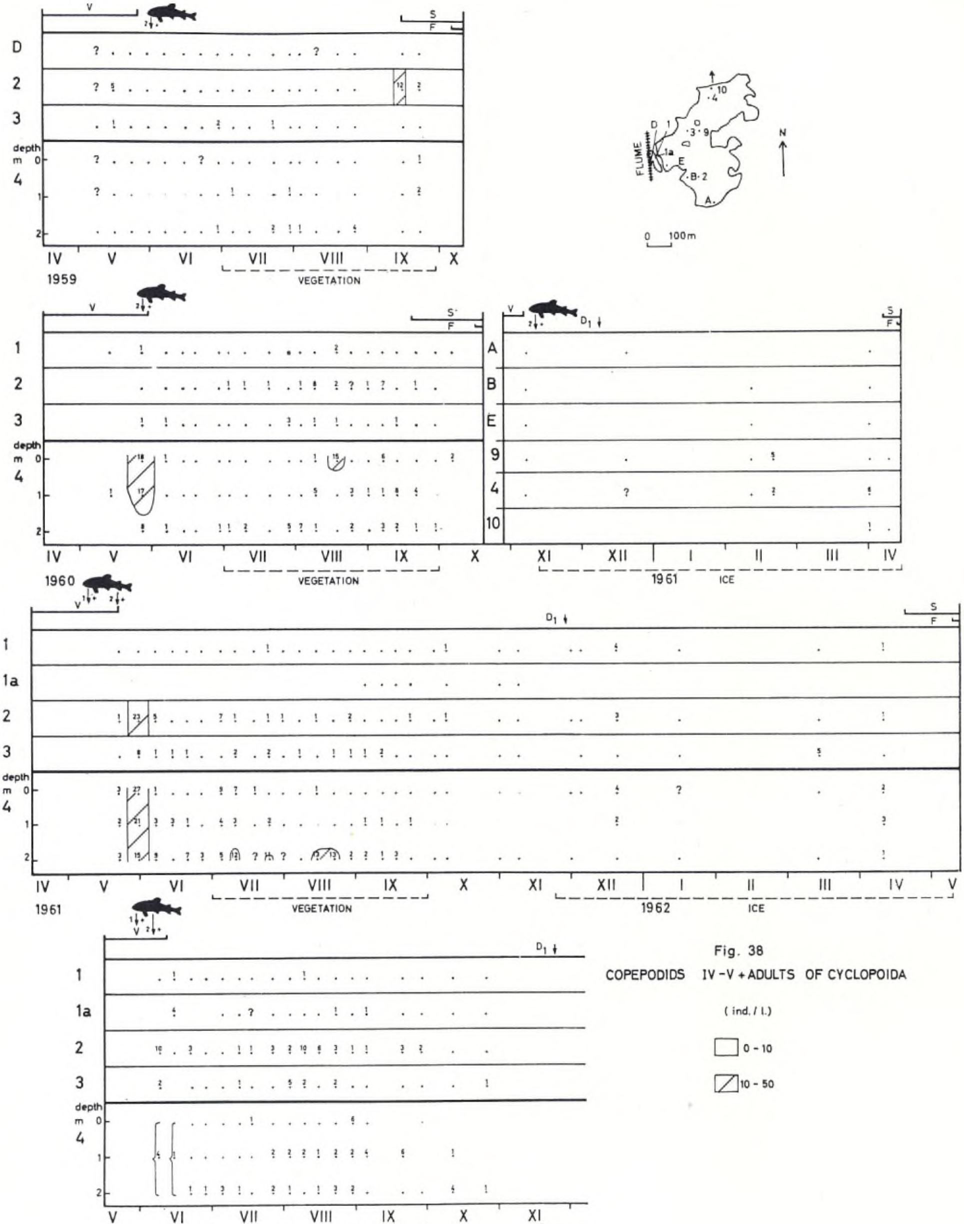


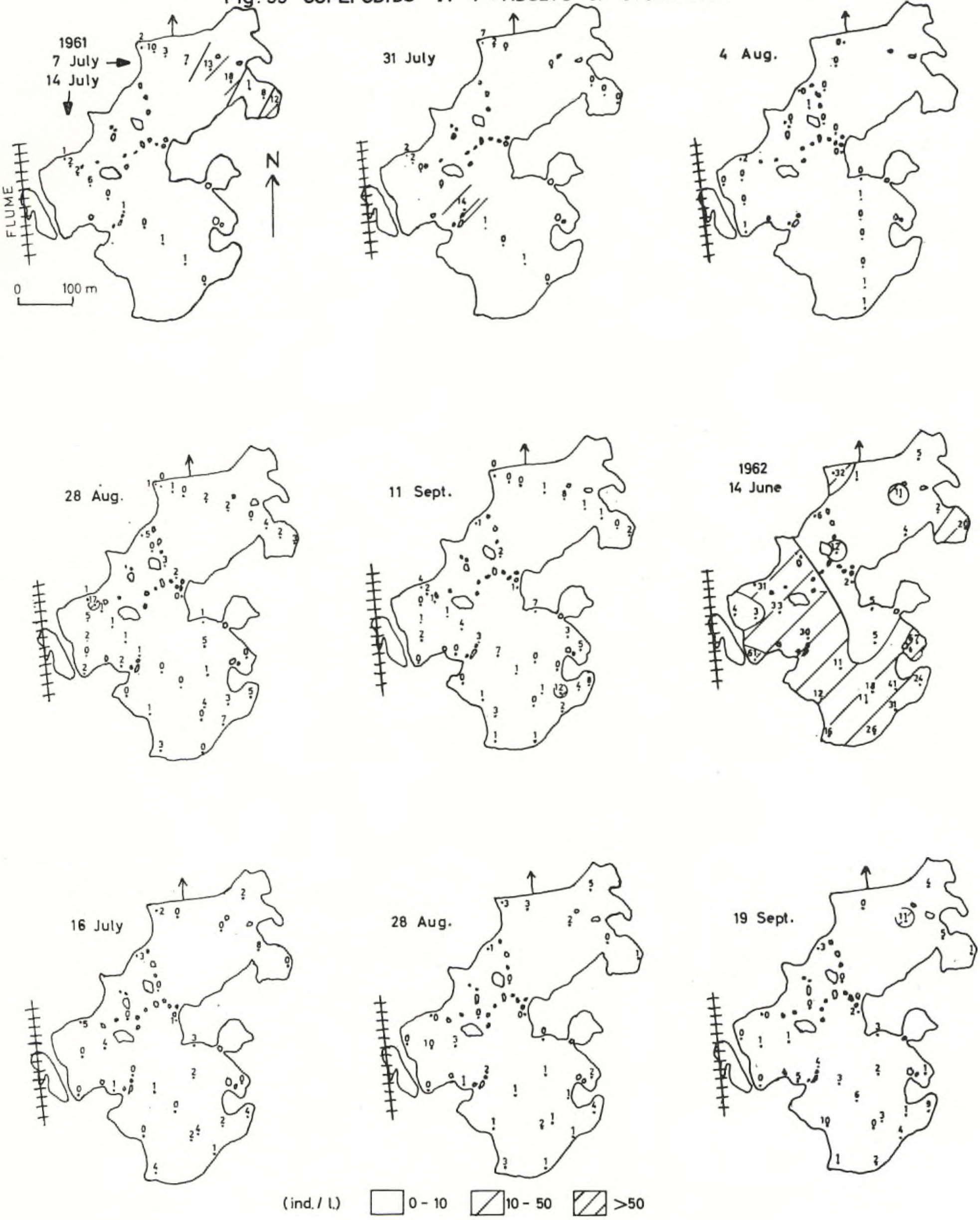
Fig. 38

COPEPODIDS IV-V + ADULTS OF CYCLOPOIDA

(ind./l.)

differences in water-chemical conditions were greatest in September. The observed higher values of biomass may be caused by the different environmental factors. At the same time the standing crop of zooplankton in the northern part of the pond, where the pond is free from vegetation and where

Fig. 39 COPEPODIDS IV-V + ADULTS OF CYCLOPOIDA



the chemical conditions are characterized by a mixture of the two waters, showed values lying between the two different areas.

To get information about the development of the standing crop of the whole pond, the mean values of the results obtained at sites 2, 3 and 4 have been calculated. The values for site 4 are mean values calculated from the

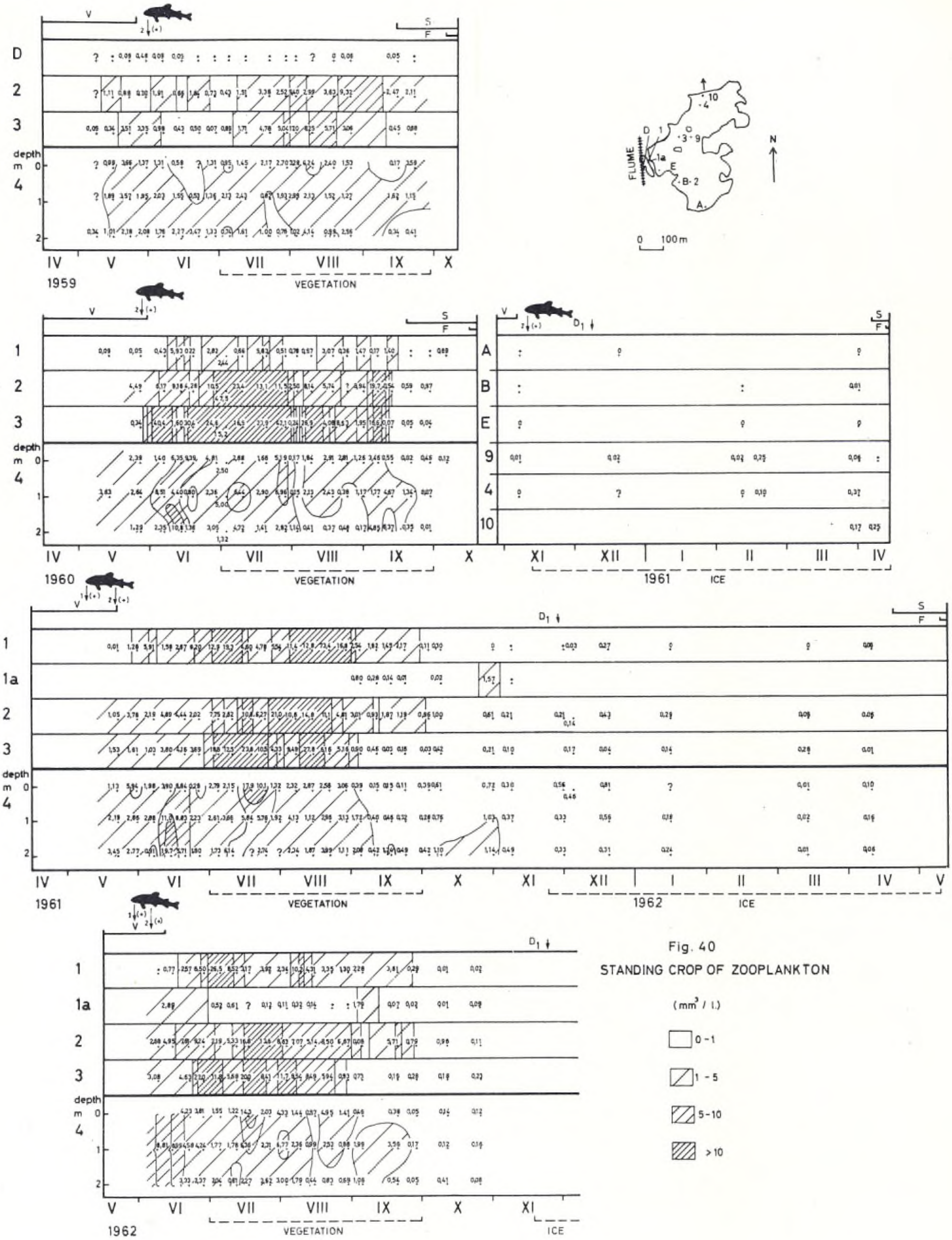
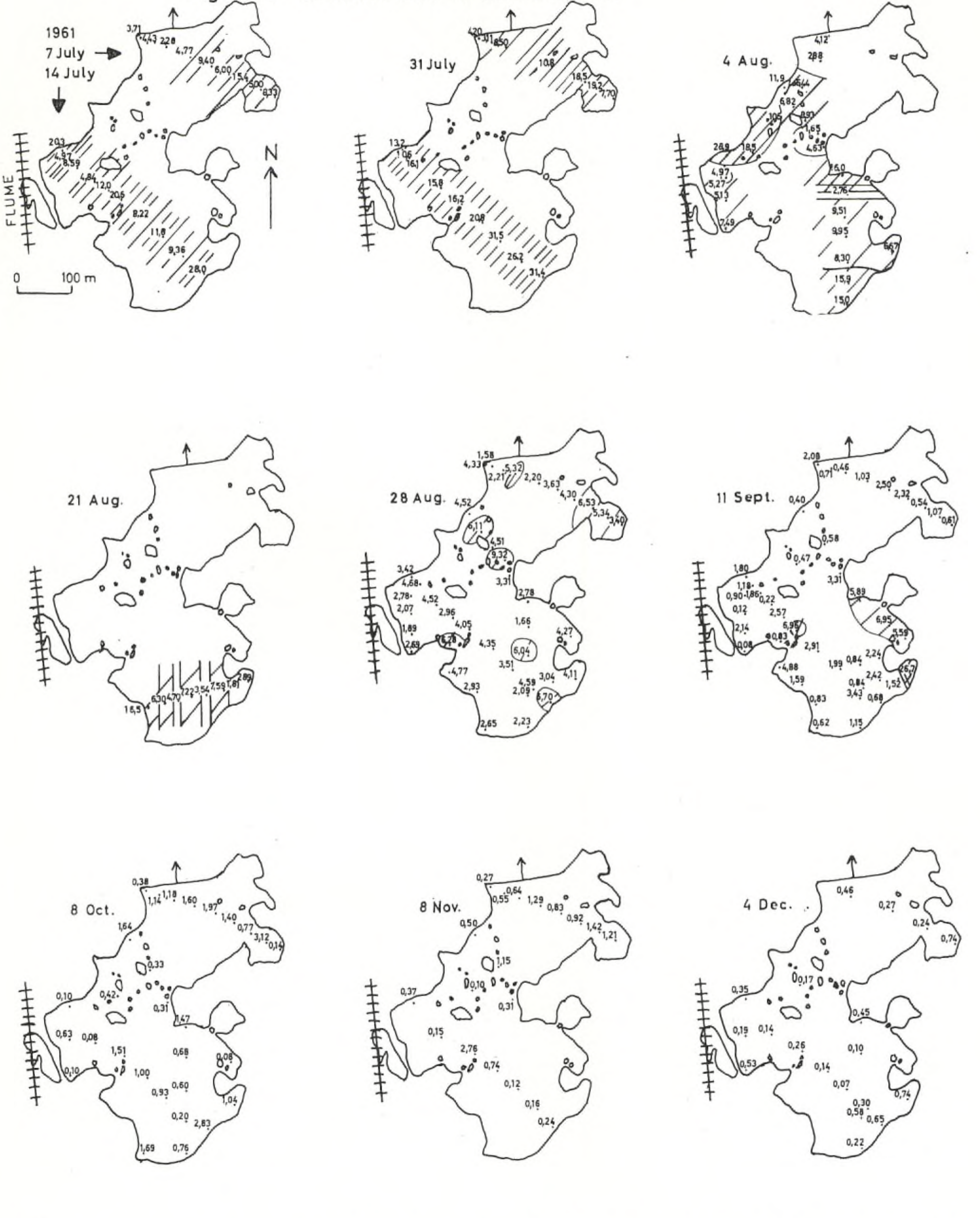


Fig. 40

STANDING CROP OF ZOOPLANKTON

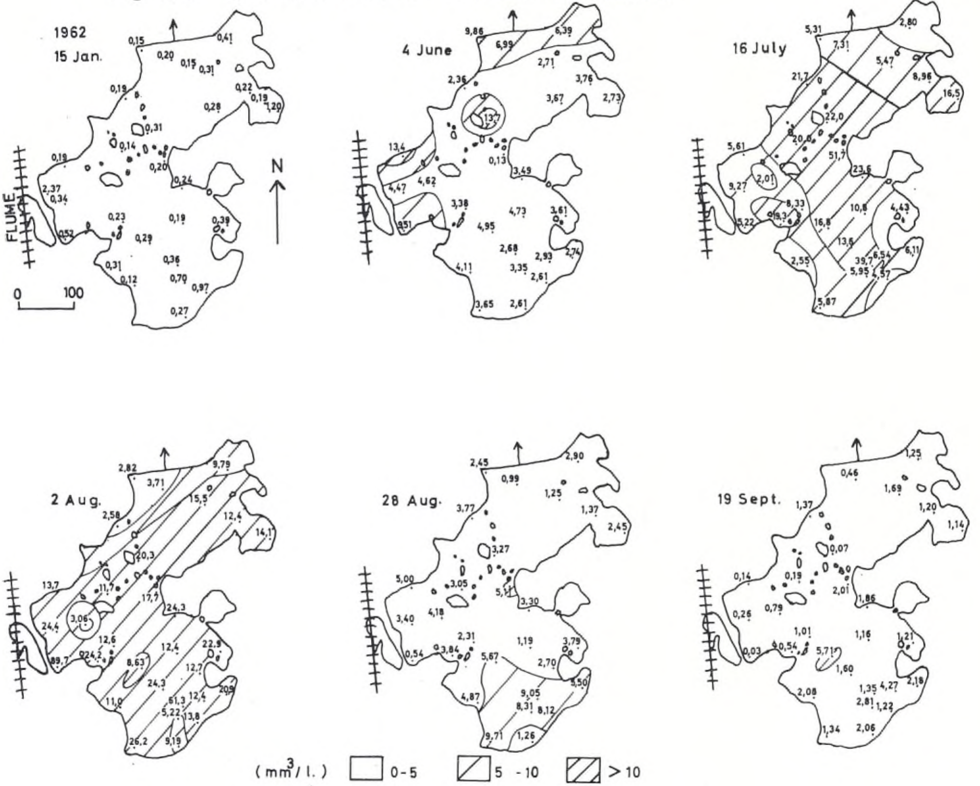
results obtained at the three depths in the following way. The whole water column from surface to bottom is regarded as consisting of two parts, from the surface to 1 m depth and from 1 m depth to the bottom. The total content of animals in these two columns is calculated (the area is that of a RUTTNER sampler) and added. Through division by the total volume of water

Fig. 41 a STANDING CROP OF ZOOPLANKTON



in the column the mean value per litre is obtained. As the biomass at the different sites differs as described above, the choice of these three sites might give an erroneous index for the whole pond. However, the values obtained can be tested against the mean values calculated from the large number of samples taken to show the horizontal distribution. These last-mentioned mean values are obtained from about 20—30 samples each time.

Fig. 41 b STANDING CROP OF ZOOPLANKTON cont'd.



In Fig. 42 a and b is shown the comparison between the mean values obtained in 1961 (a) and 1962 (b) from the three sites (given as a curve) and the 20—30 sites used to show the horizontal distribution (given as black circles within a triangle). Of the 14 black circles only 1 falls somewhat outside the curves. Thus one can assume that the mean value from the three sites give truly representative information as to the development of the standing crop of zooplankton in the pond.

In Fig. 42 c the development of the standing crop of zooplankton in Hyttödammen in the different years of investigation is compared, and also contrasted with the values found by NAUWERCK (1963) in Lake Erken. From the Figure it can be seen that, omitting the uncertain results from 1959, some maxima seemed to appear every year, even though the maxima differ in order of size. There seemed to be about 4—5 succeeding maxima in the course of the summer, due to significant oscillations in the biomass of zooplankton. They were to be found at the beginning of June, at the end of June and beginning of July, at the end of July, at the beginning and in the middle of August, and perhaps also in September. It seems as if the

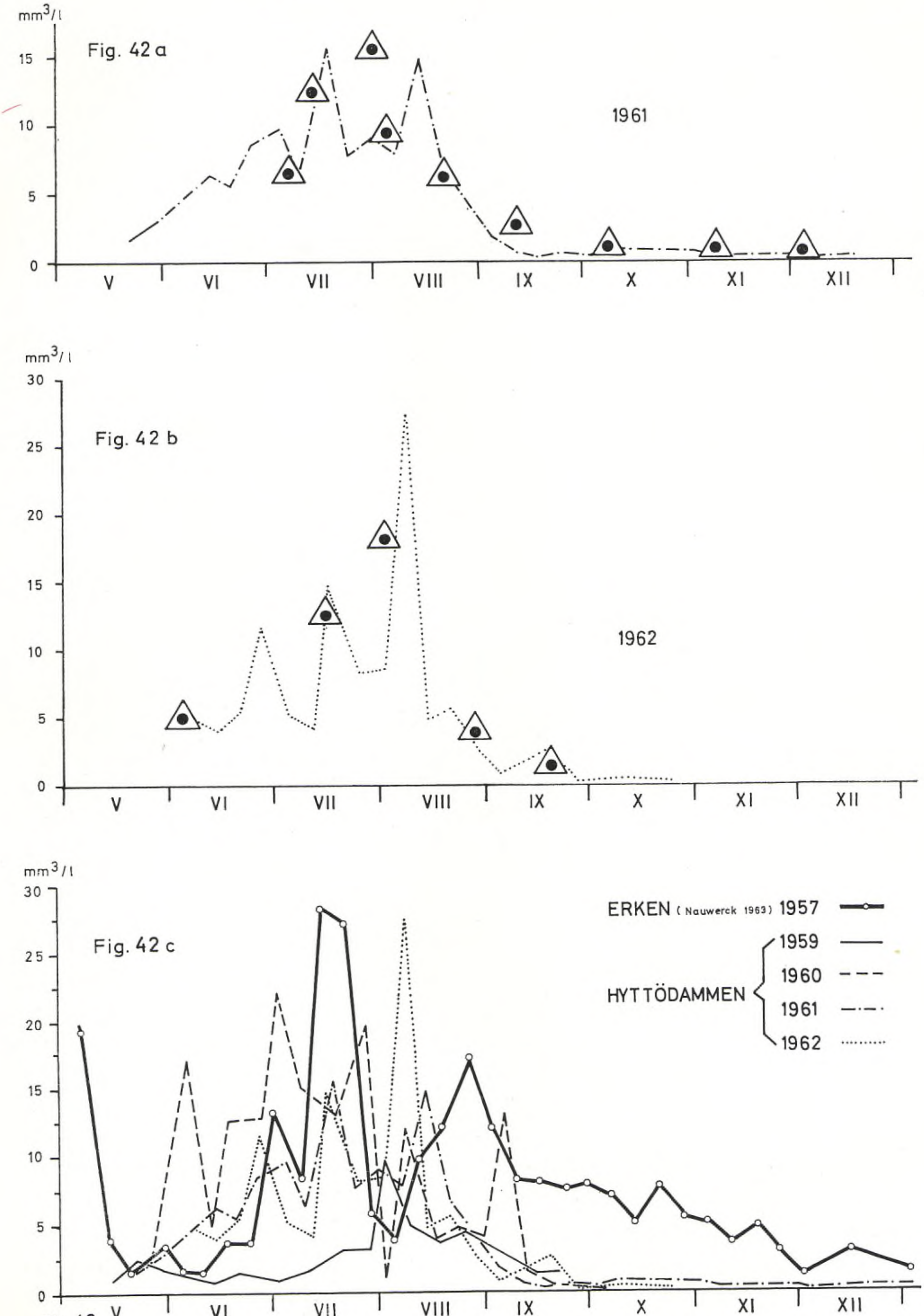


Fig. 42
Mean values of the volume of standing crop of zooplankton in Hyttödammen for different years and in Lake Erken. Further explanations in text.

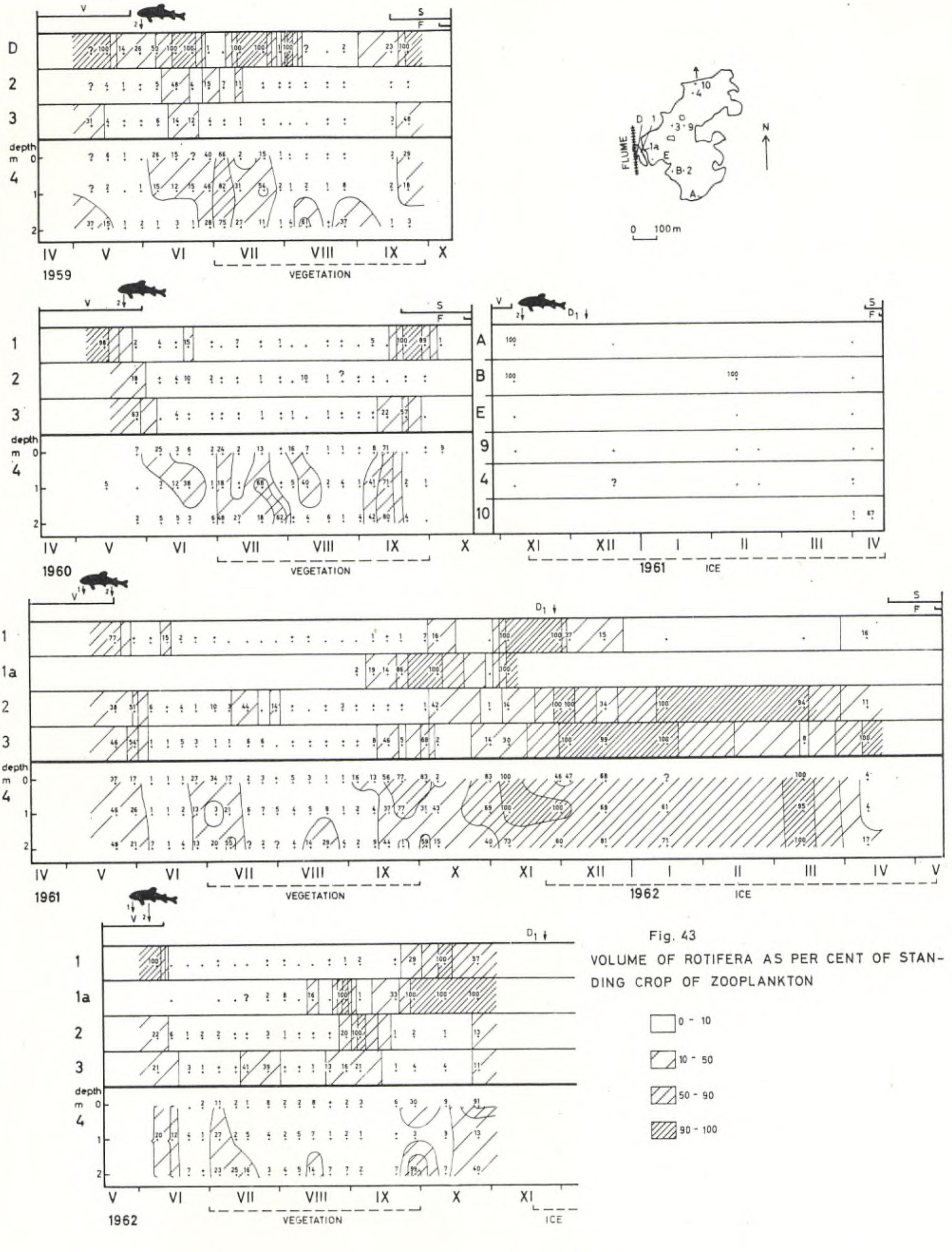
described phenomena in the zooplankton differ from those found by NAUWERCK. He found two large peaks in the summer stagnation period, of which the first, in July, was dominated by *Eudiaptomus graciloides* and the second, in August, by *Diaphanosoma* and *Ceriodaphnia*. In Hyttödammen the succeeding maxima were caused partly by a succession of different species and partly by a succession of generations within one species. In Lake Erken the generations overlapped each other so that no oscillation due to their succession could be observed, and the curve was even.

A significant difference in the development of the biomass from the end of September onwards is also to be found when comparing Hyttödammen and Lake Erken. In Hyttödammen a very rapid decrease in the end of September occurred, but in Lake Erken the decrease towards the end of the year went more slowly. Probably this difference is due to the different rate of change of the temperature when the cooling of a small water mass such as Hyttödammen is compared with the cooling of a large one such as Lake Erken. Even if the standing crop of zooplankton in Hyttödammen oscillates much more than in Lake Erken, a calculated value of mean standing crop from June to September gives about the same order of size in both but still lower values in Hyttödammen. When considering this, it must be kept in mind that the values from Lake Erken are mean values from a sampling station that is ten times deeper than those in Hyttödammen. As a rule the biomass of zooplankton decreases in the deeper layers, which means that the values from Hyttödammen are slightly favoured. Thus, the mean value from Lake Erken, based on 17 samples in 1957, was 10.20. In Hyttödammen the values for the years 1960, 1961 and 1962 were 9.34, 6.33, 6.93, based on 17, 17 and 16 samples. However, these values do not say anything about the productivity in the two compared materials.

The volume of the *Rotatoria* was low as a rule. In Fig. 43 their part of the standing crop of zooplankton volume is shown. The highest values were found in the spring after the filling of the pond and from October throughout the winter, due to an increase in the numbers of rotifers but also above all to the absence of most of the *Cladocera* and *Copepoda*. In the summer a tendency towards higher values at site 4 than at the other sites can be observed. This is due to the occurrence of *Polyarthra major*.

The *Cladocera* (Fig. 44) was the most important group of the standing crop of zooplankton in the summer at all the sites, but with some variation between sites and between years. At site 1 the zooplankton often consisted only of *Cladocera*. At sites 2 and 3, where vegetation was found, the values as a rule were higher than 60 %, and often over 90 %. At site 4 the values as a rule were higher than 50 % but rarely over 90 %.

The *Copepoda* (Fig. 45) ranked in importance between the *Rotatoria* and the *Cladocera*, as a rule making up between 10 and 40 % of the biomass. This group was regularly more numerous at site 4 than at the other sites, and was almost absent at site 1.



5. Zooplankton in the organic drift into the pond

In the observations of MÜLLER about organic drift in streams (1955) it was shown that even zooplankton organisms from the pelagic zone in lakes were transported. Here only the role of zooplankton in the organic drift will be treated. In the observations made by ARNEMO (1960), it was shown that

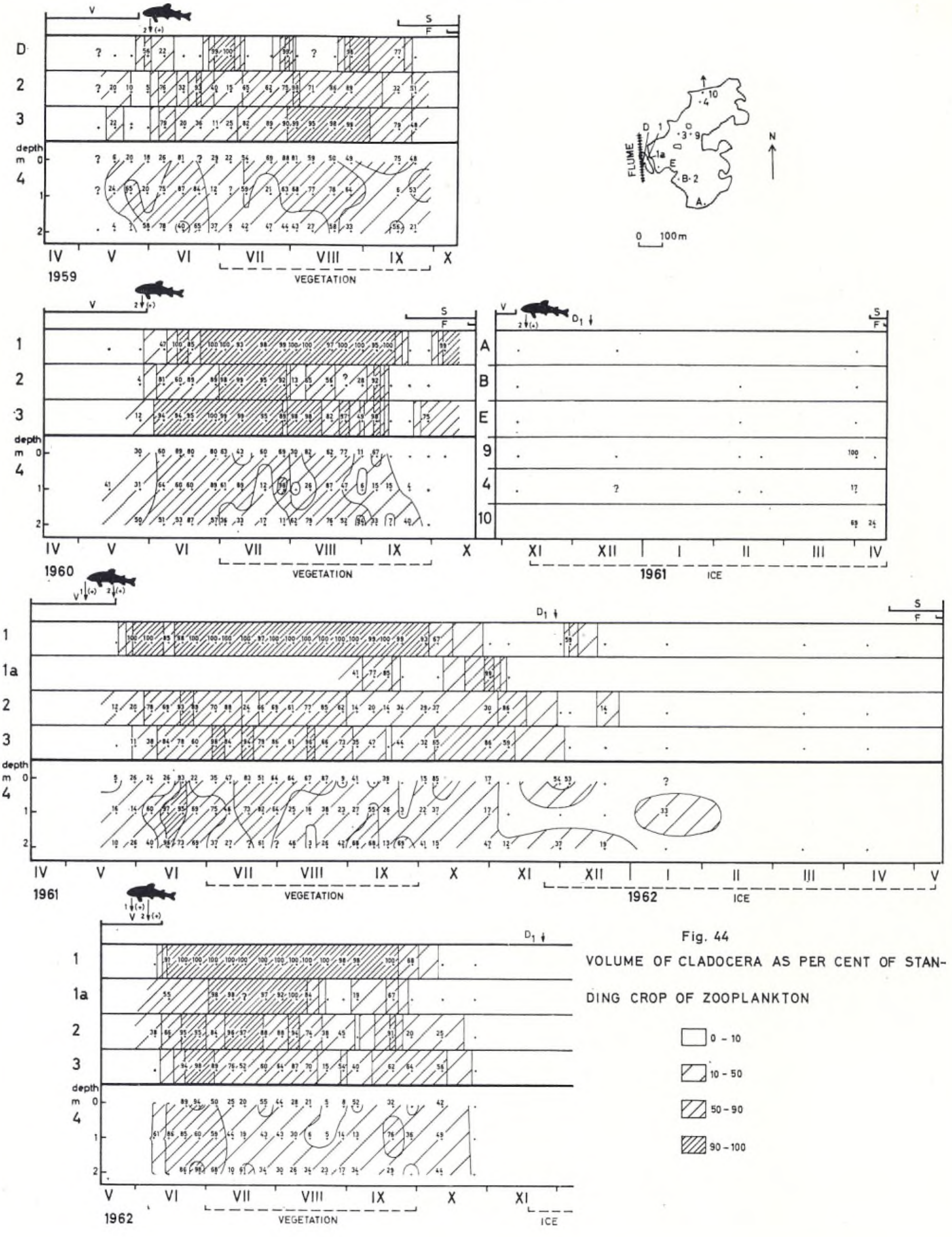


Fig. 44

VOLUME OF CLADOCERA AS PER CENT OF STANDING CROP OF ZOOPLANKTON

the drift of zooplankton via the flume to the pond was very small and was dominated by *Rotatoria.* This is also shown in the various Figures in this article showing the distribution of the species. In all these Figures the values from 1959 are found at site D. While the importance of the drift of zooplankton in the flume was shown to be very slight, the importance of the

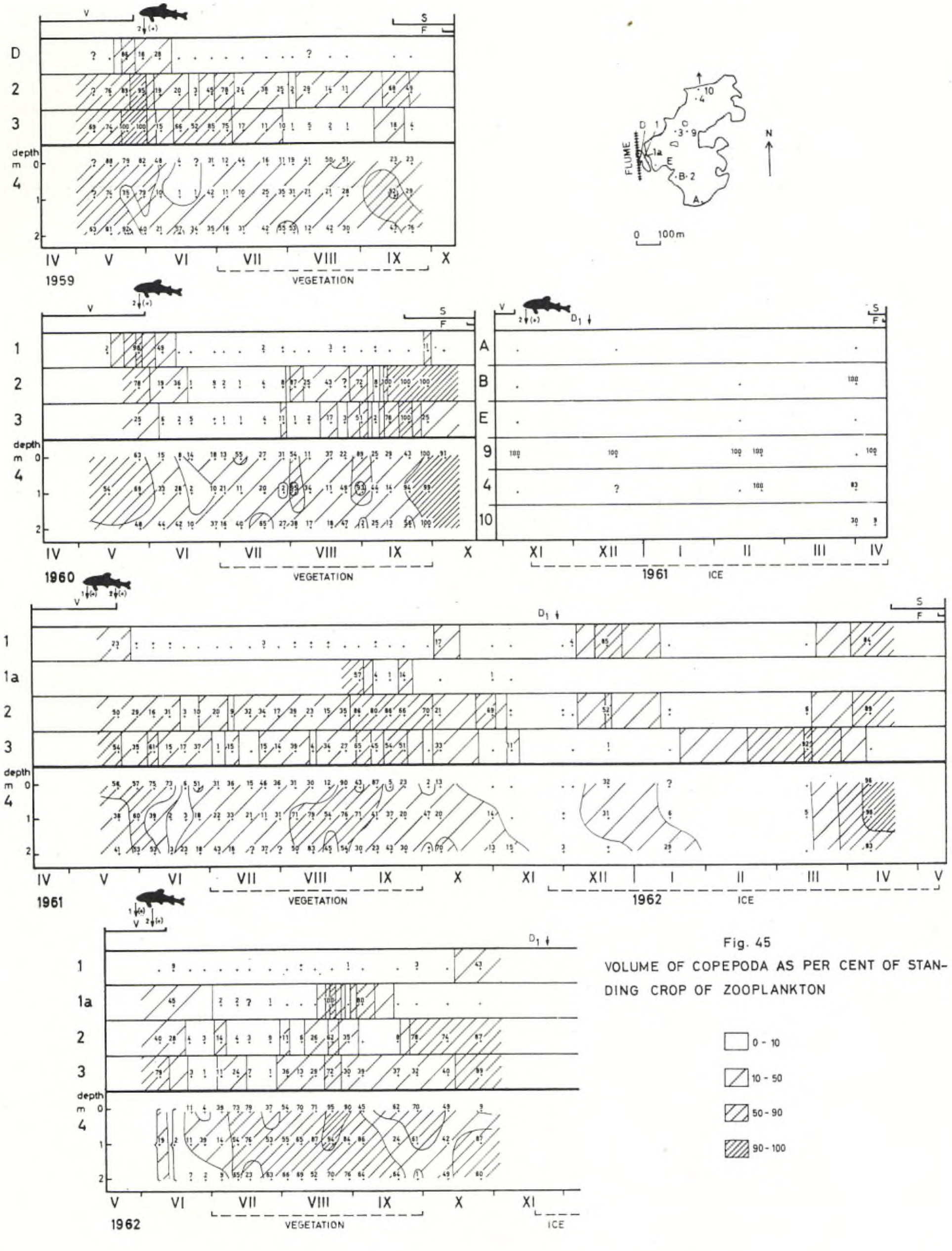


Fig. 45
VOLUME OF COPEPODA AS PER CENT OF STANDING CROP OF ZOOPLANKTON

inlet pond had to be taken into consideration. Thus, the drift from the inlet pond into Hyttödammen had to be examined.

In the inlet pond where site 1 is situated, the zooplankton community (see p. 260) consists almost only of *Cladocera,* which often showed high standing crop values. No fish were placed there and no fish were permitted to migrate from Hyttödammen. As it was desirable to take advantage of the production of the inlet pond via organic drift, fish meal was regularly added at site 1 to increase the production and thereby also the drift. However, as can be seen in all the Figures, (see under site 1 a), the drift of zooplankton to Hyttödammen was very small, compared with the number of individuals occurring in the inlet pond. The velocity of the short stream fluctuates greatly, reflecting the varying quantities of inflow from the flume. As was shown by BROOK and WOODWARD (1956) some species of the *Crustacea* show an avoidance reaction when they are about to be carried away by the outflow. The desired effect of the food supply could be increased if the flow of water through the inlet pond was more rapid.

However, some organic drift can already be observed under the prevailing conditions, partly from the Figures and partly from observations in the field. The standing crop (Fig. 40) showed low values by quantities per litre but when the quantities passing per unit of time are considered, the values become of some importance. The maximum flow is about 100 l./sec but it can decrease to about 10 l./sec. Of the zooplankton found in the samples, the *Cladocera* and the *Rotatoria* (Figs. 43 and 44) were most common. The *Copepoda* (Fig. 45) were less significant, reflecting the conditions at site 1 already described above (p. 260). This material is too sparse to permit any analysis of differences between the zooplankton community in the inlet pond and the community occurring in the organic drift, and therefore of the correlation between the velocity of the outflow and qualitative composition of the zooplankton in the organic drift.

Through observations in the field it can be verified that an organic drift was present. A shoal of some thousands of fishes could be observed swimming in the stream immediately at the outflow into Hyttödammen and from time to time they made short, rapid attacks against drifting objects. This will be dealt with in detail in a later article about the food of the fish.

6. Distribution close to the shore

As noted above (p. 235), Hyttödammen not only showed a zooplankton commynity that was typical for ponds and littoral conditions but also in some ways showed pelagic conditions typical of lakes. Some further information about the zooplankton on these points can be given here, based upon the results obtained from samples taken on August 21, 1961. Samples were taken at site 4 and at some other sites lying along a line northwards from site 4 (cf. ARNEMO 1964, Fig. 2). The last sample was taken at the dam where the depth was 0.1 m. All the sites lie within the area of the pond that is not covered with vegetation. The lack of vegetation even close to the shore at the dam is due to the fact that the bottom consists only of the stones making up the dam. With the exception of site 4 the sites lie at distances from the shore of 4.0, 1.0, and 0.1 m, where the depths are 2.2, 0.4 and 0.1 m.

The results show that the standing crop of zooplankton was about the same at all the sites with 1—5 mm³/l. except at the site located closest to the shore with 22.6 mm³/l. The difference is almost wholly due to the different numbers of *Bosmina* in the samples (cf. cited literature, p. 233). Closest to the shore there were 351 ind./l. of *Bosmina,* which is about the same order of size as in the samples taken among the vegetation (=littoral part of the pond). In the other samples the numbers were about the same (10—30 ind/l.) as those found in areas free from vegetation (=pelagial part of the pond). The observations on the occurrence of *Heterocope appendiculata* in the samples to some extent reinforce the impression of a very small littoral zone closest to the shore in areas free from vegetation. This species was found in the sample taken 4 m from the shore, but not in the two samples taken closer to the shore.

7. Additional comments on environmental factors and zooplankton

(a) *Temperature.*

The temperature cycle has been described by ARNEMO (1964, pp. 19—25). As is characteristic for a small and shallow water mass such as Hyttödammen, it heats and cools rapidly in response to the large variations in air temperature. Thus, there may be a shorter time of development for some species compared with their development in a lake (see p. 240 for the copepodid stages). This would be especially true for those species occurring soon after the filling of the pond in the spring, when a rapid heating is observed. In addition, this rapid increase of temperature may have harmful effects and may contribute to shortening the life span of some species (see p. 227, *Holopedium gibberum*). In the summer the larger variations in the temperature in a pond most probably affects warm water forms harmfully so that they do not develop a large population (see p. 223—5, *Diaphanosoma brachyurum*). The curve of the biomass of zooplankton shows many peaks in the summer (see p. 258), caused by unequal generation size and the succession of species, which in turn may be an effect of temperature. However, the variation in the populations of all the species might also be due to an indirect influence of the temperature, namely that upon the development of food organisms of the zooplankton.

ARNEMO (1964, Fig. 6) observed a horizontal transport of water in Hyttödammen on some occasions. In lakes this transport has also meant a transport of the organisms giving results that would have been very difficult to explain if the temperature (even in horizontal directions) had not been measured (AXELSON 1961, SCHRÖDER 1962 a). In Hyttödammen the stratification is not of the same order of size as in a lake and the vertical distribution of the standing crop of zooplankton is too weak to give any information as to the importance of this factor for the horizontal distribution of the organisms. Compare Fig. 41 in this article and Fig. 6 in ARNEMO 1964.

(b) *Chemical conditions.*

As was described by ARNEMO (1964) Hyttödammen receives water from two sources, namely from the river Dalälv and from some springs opening in the pond (*op.cit.,* p. 30 ff.). These two waters differ very much in chemical composition (*op.cit.,* p. 41) and when the vegetation has grown up it hinders horizontal mixing so that a horizontal heterogeneity may develop. Drawing rough limits, one can say the parts of the pond with dense vegetation may be divided into a Dalälv-influenced part in the south-west and a spring-influenced part in the south-east. When discussing differences in distribution of some species of zooplankton, it must be kept in mind that without laboratory tests it is hardly possible to say whether an observed tendency is due to a preferring or avoiding reaction or to some other effect. For species occurring only in the Dalälv-influenced part of the pond, another possible explanation is that these were transported to the pond from the Dalälv and are beginning to establish a population.

Species that are to be found in higher numbers in the spring-influenced part and to some extent in the adjoining region of the Dalälv-influenced part are: *Conochilus spp.* (see p. 223), *Diaphanosoma brachyurum* (see p. 223), *nauplii* and copepodids I—III of *Heterocope appendiculata* (see p. 240—1), copepodids IV—V and adults of *Eudiaptomus graciloides* (see p. 246—7), and *nauplii* of the *Cyclopoida* (see p. 249). Moreover, the standing crop of zooplankton (see p. 253) showed higher values in the same border area and the greatest differences were observed in September, when the chemical differences were greatest. However, it is still impossible to say anything definite about the influence of chemical conditions upon the distribution, because of the limited amount of data. Noteworthy is the distribution of *Diaphanosoma brachyurum,* which differs from that of the other species mentioned above, cf. p. 223. It is also surprising to find that different stages of the *Calanoida* appear to behave differently. This observation underlines the difficulty of interpretation and makes it possible for another factor, e.g. competition for food, to be responsible for the distribution.

Keratella cochlearis is the only species that shows highest values in the Dalälv-influenced part of the pond (compare p. 209). It is most probably transported to the pond from the Dalälv and first develops a stable population in the inlet pond, where site 1 is situated. From there the population tries to widen its distribution, but is successful only in the autumn and the winter.

(c) *Vegetation.*

The higher aquatic vegetation is generally considered to support a larger zooplankton biomass than is the case in the pelagic zone. As was discussed above, (see p. 209) the vegetation also is considered to have an antagonistic effect upon the rotifers. As to the distribution of the different species, only a few showed higher values in or outside of the vegetation. *Polyarthra major* (see p. 215) was found in higher values outside the vegetation, *Holopedium gibberum* (see p. 225—7) showed a similar distribution, when this species had a maximum although the vegetation was not grown up. After the vegetation was fully grown, *Holopedium* disappeared even from site 4, probably owing to the changes in the temperature (discussed on p. 265).

Bosmina spp. (see p. 231) was about ten times more plentiful in areas with dense vegetation than in other areas. However, no differences seemed to exist between the areas with and without vegetation when the standing crops of zooplankton were compared, in spite of the dominating role of *Bosmina*. On the other hand, this does not eliminate the possibility that a higher production may be found either outside or within the vegetation. Either the values obtained in Hyttödammen diverge from the general findings about higher biomass being found within the vegetation, or possibly the whole pond must be considered littoral in that respect.

(d) *Food.*

No special investigations have been made of the feeding habits of the different species of zooplankton. Data on the occurrence of the food particles are almost completely lacking (detritus, not studied; bacteria, studied once) or are incomplete because of too long intervals between the sampling occasions (phytoplankton, see ARNEMO and NAUWERCK 1965). Thus the conclusions must be based mostly upon assumptions and are therefore very limited.

The distribution of *Polyphemus pediculus* seems difficult to explain adequately if competition for food is not taken into consideration (see p. 234). Possibly there exists a competition for food between the *nauplii* of *Heterocope* and *Eudiaptomus* (see p. 245).

In the case of the adults of the first generation of *Heterocope appendiculata*, optimal food condition probably contributed to better growth resulting in larger individuals than found at other times.

As was pointed out by NAUWERCK (1963) in Lake Erken, the standing crop of phytoplankton was much lower than that of zooplankton. Throughout the year the standing crop of zooplankton in Lake Erken, varied between 1.3 and 30 times that of phytoplankton. In Hyttödammen the corresponding values (data on phytoplankton taken from ARNEMO and NAUWERCK 1965) are given in the Table below.

Date of sampling 1962		Standing crop as mm³/l of		Phytoplankton/Zooplankton
Phytoplankton	Zooplankton	Phytoplankton	Zooplankton	
17 June	14+21 June	1.65	4.77[1]	1 : 3
9 July	11 July	0.66	4.12	1 : 6
28 ”	25 July+2 Aug.	0.46	8.30[1]	1 : 18
27 Aug.	28 Aug.	0.79	2.86	1 : 4
18 Sept.	19 Sept.	0.79	2.64	1 : 3

[1] This is a mean value based upon results obtained at the dates indicated.

Thus, in the few estimates made, there is from 3 to 18 times higher biomass of zooplankton than phytoplankton, with a mean of 4.3. NAUWERCK, with more data from Lake Erken, found a mean of 5.5. If the efficiency of conversion of phytoplankton to zooplankton is about 10 % (NAUWERCK 1963, p. 105) then the 4.3: 1 found as the ratio of the biomass of zooplankton to phytoplankton in Hyttödammen can be considered to represent a theoretical ratio of zooplankton to phytoplankton biomass of 43: 1. The turnover time for the phytoplankton, based on summer results of biomass and assimilation given by Arnemo and NAUWERCK (1965), was about 6 days. The same value for Lake Erken throughout the year was 3 days (NAUWERCK 1963). Assuming that all the phytoplankton will be consumed by the zooplankton and that the zooplankton feeds only on phytoplankton, the turnover time for the biomass of zooplankton should be about 258 days (6×43). This is quite impossible, knowing the rapid changes and peaks in the curve of biomass of zooplankton throughout the summer, and emphasizes in a higher degree than in the Lake Erken study by NAUWERCK the important role of other food objects (e.g. detritus, bacteria) for the zooplankton. Although it is only a single observation, the bacterial analysis (ARNEMO 1964, p. 89) showed higher numbers of bacteria in Hyttödammen than in unpolluted lakes in the surroundings of Uppsala (TULLANDER, pers. comm.). Thus the food conditions in Hyttödammen for the zooplankton may be somewhat better than in those lakes. Even if the influence of the predation by fish is unknown in these two investigations that have been compared, it is probable that the general results would not be changed (density of a population of bottom-fauna- and zooplankton-consuming fish in Hyttödammen was 1 ind/m^2 and was unknown in Lake Erken).

VI. Hyttödammen in different classification systems

In recent years it has been suggested (RODHE 1958) that classification of the degree of trophy should be based only upon the productivity of the investigated environment. In Hyttödammen no investigation was made of the productivity of the zooplankton, a part of the secondary production. The primary production was investigated and the results (ARNEMO and NAUWERCK 1965) show that Hyttödammen, *sensu* RODHE (1958), stands between oligotrophy and eutrophy.

In older investigations the trophic classification was based upon the dominating species and it may be of interest to compare the classification of Hyttödammen by this method with the results from the primary production. Hyttödammen will also be compared with other investigations, some of which suggested a classification based only on the zooplankton composition while rejecting completely any considerations of trophy.

In Hyttödammen, considering the percentage composition in the summer based upon the volumes, the *Rotatoria* are of little significance, even if they often show a high number of ind/l. The most important groups are the *Cladocera* and the *Copepoda*. The most frequent species are (given in order of frequency) *Bosmina spp., Heterocope appendiculata, Eudiaptomus graciloides, Holopedium gibberum* and the *Cyclopoida*. Less frequent are *Sinantherina socialis, Conochilus spp., Chydorus sphaericus, Camptocercus lilljeborgi.*

This structure in the zooplankton community was not found by GRIMÅS *et al.* (1954) in the Swedish salmon-rearing ponds that were most closely comparable to Hyttödammen. GRIMÅS found *Bosmina* and *Holopedium* to be the most numerous zooplankters in all the 5 ponds investigated, which resembles the conditions in Hyttödammen. However, GRIMÅS also found some other *Cladocera,* different ones in different ponds, to be among the dominant species, namely *Polyphemus, Ceriodaphnia pulchella, Diaphanosoma* and *Daphnia longispina var. hyalina (form. galeata)*. GRIMÅS never found *Copepoda* to be among the dominant species.

NORDQUIST (1921) found, in his investigations of ponds in the south of Sweden having different fish populations, that in the oligotrophic ponds *Bosmina obtusirostris, Daphnia longispina* and *Polyphemus pediculus,* (all *Cladocera*), dominated. In the eutrophic ponds it was characteristic to find many *Rotatoria* and some *Copepoda,* coupled with a decreasing influence of the *Cladocera.* Based upon the discussion and the results of NORDQUIST, Hyttödammen is thus to be considered as lying between oligotrophic and eutrophic conditions, even if the species that dominate it were not the same as in the studies compared.

According to WEIMANN (1942), Hyttödammen most resembles the partly eutrophic pond of type "Übergangsstufen". As to the phytoplankton, ARNEMO and NAUWERCK (1965) classified Hyttödammen in the same system as a mesotrophic, "Chrysomonadenteich". The observation by ARNEMO (1964) that the values of phosphorus were so high that they gave an impression that Hyttödammen was polluted is also noteworthy.

Thus, according to the older systems, Hyttödammen should be classified as moderately eutrophic.

ŠRÁMEK-HUŠEK (1962) gave a review of the pelagic *Cladocera-* and *Copepoda*-communities of the Central European waters. According to that system Hyttödammen resembles both the *"Daphnio-Diaptometum graciloides"* and the *"Daphnio-Bosminetum coregoni"*, even if the *Daphnia* in Hyttödammen plays a subordinate role and some of the species given as characterizing the types are lacking. These communities of zooplankton are most commonly to be found in large lakes but sometimes also occur in large ponds. Before classifying Hyttödammen in this scheme we have to keep in mind that the classification concerned only pelagic species. However, the example serves to emphasize the impression one gets of Hyttödammen as showing features both of a lake and a pond. ŠRÁMEK-HUŠEK also discussed ponds in his classification, but the communities found by him do not resemble the Hyttödammen community very much.

VII. Summary

The zooplankton composition in Hyttödammen (a 12-hectare pond for rearing of first-summer or one-year-old-salmon) was investigated qualitatively and quantitatively in 1959—62. Samples were taken weekly from the time of filling of the pond in mid- or late May to mid-September and thereafter throughout the winter at about monthly intervals. By means of these samples the temporal and to some extent the spatial distribution, together with the vertical distribution at the deepest part of the pond (2.2 m), were investigated. In the summer the zooplankton was dominated volumetrically by *Cladocera* (*Bosmina coregoni*+*longirostris* and *Holopedium gibberum*) and after that the groups of importance were the *Copepoda* (*Heterocope appendiculata, Eudiaptomus graciloides* and *Cyclopoida*) and the *Rotatoria* (*Sinantherina socialis, Conochilus unicornis*+*hippocrepis*). In the winter the *Rotatoria* dominated (*Synchaeta* and *Keratella cochlearis*) and the *Copepoda,* together with the *Cladocera*, were more or less absent. No vertical stratification of any species could be observed.

In 1961—62 the horizontal distribution was investigated by monthly sampling at about 20—30 sites. These samples showed that some species had an irregular distribution which, it was suggested, was due to the differing distribution of the higher aquatic vegetation in the pond. Thus *Bosmina coregoni*+*longirostris* occurred in higher numbers within the vegetation and *Polyarthra major* occurred in higher numbers outside the vegetation. The differing chemical conditions within the pond did not cause any irregular distribution, except for a possible effect in the case of *Diaphanosoma brachyurum.*

Temperature seems to affect the populations in two ways: the rapid heating in May-June caused a more rapid development of the populations that developed first, and the rapid changes during the summer probably influenced the warm-water forms more than other forms, so that the latter did not develop a large population.

Competition for food and predation exerted by *Heterocope appendiculata* probably influenced the carnivore *Polyphemus pediculus* so that it never developed a large population. The absence of this species as a dominant zooplankter is also discussed as it often dominates the littoral regions in oligotrophic lakes and all parts of oligotrophic ponds. Thus the observations on the absence of *P. pediculus* combined with the occurrence of the pelagic

species *Heterocope appendiculata* and *Eudiaptomus graciloides* indicates that the zooplankton of Hyttödammen shows characters typical of lakes.

Biometrical analysis of *Heterocope appendiculata* gave higher values than those earlier reported in the literature.

The picture of the standing crop in Hyttödammen was characterized by about 4—5 maxima due to rapid changes in generations within the species and to succession of species, as compared with 2 maxima in Lake Erken. The calculated mean standing crop in the summer was about the same in both these environments. In Lake Erken, the decrease during autumn proceeded slowly, but in Hyttödammen it was rapid in late September.

The ratio between the standing crop of phytoplankton and that of zooplankton in the summer in Hyttödammen seemed to be about the same as in Lake Erken. Using the same methods of calculation and comparison applied in the Lake Erken study to estimate the standing crop and turnover times, and knowing that only part of the phytoplankton serves as food for the zooplankton, it is clear that other food sources (detritus, bacteria) are used by the zooplankton.

As no investigation was made of the productivity of the zooplankton, Hyttödammen cannot be classified in this way. On the basis of older methods using the composition of the zooplankton, Hyttödammen stands somewhere between oligotrophy and eutrophy.

VIII. Acknowledgments

I acknowledge with pleasure and gratitude the many years of valuable instruction by Professor W. Rodhe, head of the Institute of Limnology, Uppsala. He has also read the manuscript critically.

During planning of the investigation and the field work I have received most valuable support and encouragement from Dr. C. Puke, the Royal Fishery Board of Sweden.

It is a pleasure also to acknowledge the inspiring cooperation of Mr. N. G. Steffner, head of the Hatchery at Älvkarleö, and his staff during the whole of the field work.

Dr. B. Bērziņš, Aneboda, determined some of the *Cladocera* and gave valuable suggestions during the planning of this work and the writing of this article.

Docents A. Nauwerck and B. Pejler helped me in many valuable ways during the work on the manuscript.

Dr. U. Einsle, Konstanz, determined the *Cyclopoida*.

Miss L. Liliedahl and Mr. S. Åhrberg made the drawings.

Mr. J. Karlsson assisted me with microscopic analysis.

Dr. J. Hobbie helped me with the English version.

To all these persons I wish to express my sincere thanks.

Financial assistance for the field work was given by the Royal Fishery Board of Sweden and the foundations "Främjande av ograduerade forskares vetenskapliga verksamhet" of the University of Uppsala and "Hierta-Retzius' fond för vetenskaplig forskning" of the Royal Academy of Sciences.

Finacial assistance for the analysing and the publishing of the material was given by the "P. E. Lindahls stipendiefond" of the Royal Academy of Sciences.

IX. References

Allgén, C., 1933. Hjuldjur (Rotatoria) från sjö- och dammområdet vid Aneboda. *Skrifter utg. av Södra Sveriges Fiskeriförening 1933 (2): 57—79.*

— 1935 a. Rotatorien aus dem See- und Teichgebiet bei Aneboda (Südschweden). *Arch. f. Hydrob. 27: 416—435.*

— 1935 b. Rättelser och tillägg till Allgén, C.: Hjuldjur (Rotatoria) från sjö- och dammområdet vid Aneboda. *Skrifter utg. av Södra Sveriges Fiskeriförening.*

Alm, G., 1916. Faunistische und biologische Untersuchungen im See Hjälmaren (Mittelschweden). *Ark. f. zoologi 10, 18.*

Amrén, H., 1964. Ecological studies of zooplankton populations in some ponds on Spitsbergen. *Zool. Bidr. Uppsala 36: 161—191.*

Arnemo, R., 1960. Limnologiska studier i Hyttödammen 1959. *Vandringsfiskutredn. Meddel. 11/1960.*

— 1964. Limnological studies in Hyttödammen. 1. Physical and chemical conditions. *Rept. Inst. Freshw. Res., Drottningholm 45: 5—93.*

— och Norlin, Å., 1962. Om vegetation och miljö i Hyttödammen vid Älvkarleby. *Skrifter utg. av Södra Sveriges Fiskeriförening 1959—1960: 42—50.*

— and Nauwerck, A., 1965. Limnological studies in Hyttödammen. 2. Phytoplankton and its production. *Rept. Inst. Freshw. Res., Drottningholm 46*: 141—166.

Axelson, J., 1961. Zooplankton and impoundment of two lakes in northern Sweden (Ransaren and Kultsjön). *Rept. Inst. Freshw. Res., Drottningholm 42: 84—168.*

Barthelmes, D., 1963. Fischereibiologie grosser Karpfenabwachsteiche in der Lausitz unter besonderer Berücksichtigung der Nährtierbestände und ihrer Ausnutzung durch die Karpfen. *Zeitschr. Fischerei, 11 (5/6): 321—451.*

Bērziņš, B., 1950. Om rotatoriefaunan i dammarna vid fiskeriförsöksstationen i Aneboda. *Skrifter utg. av Södra Sveriges Fiskeriförening 1949, 102—122.*

— 1956. Rotatoriefaunan i Aneboda fiskdammar. *Skrifter utg. av Södra Sveriges Fiskeriförening 1954—1955: 31—37.*

— 1958. Ein planktologisches Querprofil. *Rept. Inst. Freshw. Res., Drottningholm 39: 5—22.*

Brook, A. J., and Woodward, W. B., 1956. Some observations on the effects of water inflow and outflow on the plankton of small lakes. *J. Animal Ecol. 25: 22—35.*

Burckhardt, G., 1944. Verarmung des Planktons in kleiner Seen durch Heterocope. *Z. Hydrologie Hydrobiol. Komm. Schweiz. Naturforsch. Ges. 10 (1): 121—124.*

Carlin-Nilsson, B., 1935. Rotatorien aus dem Teichen bei Aneboda. Mit Kritik eines Aufsatzes von Carl Allgén. *Arch. f. Hydrob. 28: 310—317.*

Carlin, B., 1943. Die Planktonrotatorien des Motalaström. Zur Taxonomie und Ökologie der Planktonrotatorien. *Meddel. fr. Lunds Univ. Limnologiska inst. 5.*

Edmondson, W. T., 1960. Reproductive rates of rotifers in natural populations. *Mem. Ist. Ital. Idrobiol. 12: 21—77.*

Ekman, S., 1904. Die Phyllopoden, Cladoceren und freilebenden Copepoden der nordschwedischen Hochgebirge. *Zool. Jahrb. Abt. Syst. Geogr. Biol. Thiere 21.*

— 1964. Die jährliche Populationsentwicklung des planktischen Kopepoden *Diaptomus graciloides* im subarktischen Nord-Schweden. *Zool. Bidr. Uppsala 36: 277—293.*

ELSTER, H.-J., 1936. Einige biologische Beobachtungen an *Heterocope borealis* FISCHER (=*H. weismanni* Imhof). *Int. Revue ges. Hydrobiol. 33: 357—433.*

FREIDENFELT, T., 1913. Zur Biologie von *Daphnia longiremis* SARS und *Daphnia cristata* SARS. *Int. Revue ges. Hydrobiol. 6: 229—242.*

— 1921. Undersökningar över zooplankton. In: Klotentjärnarna. *Meddel. fr. Kungl. Lantbruksstyr. 232.*

GERKING, S. D., 1962. Production and food utilization in a population of bluegill sunfish. *Ecol. Monogr. 32: 31—78.*

GRIMÅS, U., 1963. Reflections on the availability and utilization degree of bottom animals as fish food. *Zool. Bidr. Uppsala 35: 497—503.*

— *et al.,* 1954. Bergeforsdammarna 1952 och 1953. *Vandringsfiskutredningens Meddel. 7/ 1954.*

GRYGIEREK, E., 1962. The influence of increasing carp fry population on crustacean plankton. *Roczniki Nauk Rolniczych 81: B Zootechniczna: 189—210.*

HAMILTON, J. D., 1958. On the biology of *Holopedium gibberum* Zaddach (*Crustacea Cladocera*) *Verh. int. Ver. Limnol. 13: 785—788.*

HASLER, A. D. and JONES, E., 1949. Demonstration of the antagonistic action of large aquatic plants on algae and rotifers. *Ecology 30 (3): 359—364.*

HAYNE, D. W. and BALL, R. C., 1956. Benthic productivity as influenced by fish predation. *Limnol. Oceanogr. 1 (3): 162—175.*

HRBÁČEK, J., 1958. Typologie und Produktivität der teichartigen Gewässer. *Verh. int. Ver. Limnol. 13: 394—399.*

— *et al.,* 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. *Verh. int. Ver. Limnol. 14: 192—195.*

IVLEV, V. S. 1961. Experimental ecology of the feeding of fishes. New Haven 1961.

JOHNSON, W. E., 1961. Aspects of the ecology of a pelagic, zooplankton-eating fish. *Verh. int. Ver. Limnol. 14: 727—731.*

LANG, K., 1928. Beiträge zur Kenntnis der Süsswasserrotatorien Schwedens. *Lunds Univ. Årsskrift N. F. Avd. 2 (23): 13.*

LELLAK, J., 1957. Der Einfluss der Fresstätigkeit des Fischbestandes auf die Bodenfauna der Fischteiche. *Z. Fischerei 6 (8): 621—633.*

LILLJEBORG, W., 1900. *Cladocera* Sueciae. *Nov. Acta Reg. Soc. Scient. Upsal. 19.*

LINDSTRÖM, T., 1952. Sur l'écologie du zooplancton crustacé. *Rept. Inst. Freshw. Res., Drottningholm 33: 70—165.*

— 1958. Observations sur les cycles annuels des planctons crustacés. *Rept. Inst. Freshw. Res., Drottningholm* 39: 99—145.

LÖTMARKER, T., 1964. Studies on planktonic crustacea in thirteen lakes in northern Sweden. *Rept. Inst. Freshw. Res., Drottningholm 45: 113—189.*

MARGALEF, R., 1955. Temperatura, dimensiones y evolución. *P. Inst. Biol. Apl. Tomo 19: 13—94.*

MÜLLER, K., 1955. Produktionsbiologische Untersuchungen in Nordschwedischen Fliessgewässern. *Rept. Inst. Freshw. Res., Drottningholm 36: 148—162.*

NAUMANN, E., 1921. Spezielle Untersuchungen über die Ernährungsbiologie des tierischen Limnoplanktons. I. Über die Technik des Nährungserwerbs bei den Cladoceren und ihre Bedeutung für die Biologie der Gewässertypen. *Lunds Univ. Årsskrift N. F. Avd. 2 (17): 4.*

— 1927. Die Definition des Teichbegriffs. *Arch. f. Hydrob. 18: 201—206.*

NAUWERCK, A., 1963. Die Beziehungen zwischen Zooplankton und Phytoplankton im See Erken. *Symb. Bot. Ups. 17: 5.*

NORDQUIST, H., 1921. Studien über das Teichzooplankton. *Lunds Univ. Årsskrift N. F. Avd. 2 (17): 5.*

PEJLER, B., 1956. Introgression in planktonic rotatoria with some points of view on its causes and conceivable results. *Evolution 10 (3): 246—261.*

— 1957 a. Taxonomical and ecological studies on planktonic rotatoria from northern Swedish Lapland. *K. V. A. Handl. 6: 5.*

— 1957 b. Taxonomical and ecological studies in planktonic rotatoria from central Sweden. *K. V. A. Handl. 6: 7.*

— 1961. The zooplankton of Ösbysjön, Djursholm. I. Seasonal and vertical distribution of the species. *Oikos 12 (2): 225—248.*

— 1962. The zooplankton of Ösbysjön, Djursholm. II. Further ecological aspects. *Oikos 13 (2): 216—231.*

— 1965. Regional-ecological studies of Swedish fresh-water zooplankton. *Zool. Bidr. Uppsala 36: 407—515.*

PUKE, C., 1949. Environment and productivity of lakes near Stockholm. *Rept. Inst. Freshw. Res., Drottningholm 29: 81—84.*

RICKER, W. E., 1937. Physical and chemical characteristics of Cultus Lake, British Columbia. *J. Biol. Bd. Can. 3 (4): 363—402.*

RODHE, W., 1958. Primärproduktion und Seetypen. *Verh. int. Ver. Limnol. 13: 121—141.*

RYLOV, W. M., 1935. Das Zooplankton der Binnengewässer. *Die Binnengewässer 15.* Stuttgart.

SARS, G. O., 1863. Oversigt af de indenlandske ferskvandscopepoder. *Videnskabsselskabets forhandlinger for 1862.*

— 1865. Norges ferskvandskrebsdyr. Første afsnit. *Branchiopoda.* I. *Cladocera Ctenopoda.. Kongl. Norske Univ. Program for 1ste halvaar 1863.*

SCHRÖDER, H. und R., 1964. Ein Beitrag zu Horizontalverteilung des Zoo- und Phytoplanktons in Querprofilen. *Mem. Ist. Ital. Idrobiol. 17: 81—101.*

SCHRÖDER, R., 1959. Die Vertikalwanderungen des Crustaceenplanktons der Seen des südlichen Schwarzwaldes. *Arch. f. Hydrob. Suppl. 25, Falkau-Schr. 4: 1—43.*

— 1962 a. Verticalverteilung des Zooplanktons und Thermokline. *Arch. f. Hydrob. Suppl. 25, Falkau-Schr. 4: 401—410.*

— 1962 b. Vertikalverteilung des Zooplanktons in Abhängigkeit von den Strahlungsverhältnissen in Seen mit unterschiedlichen Eigenschaften. *Arch. f. Hydrob. Suppl. 25, Falkau-Schr. 4: 414—429.*

SCHÄPERCLAUS, W., 1943. Der Einfluss verschiedener Faktoren auf die Mengenentfaltung der Chironomidenlarven am Teichboden. *Arch. f. Hydrob. 40: 493—524.*

— 1961. Produktionsbedingungen und Ertrag in sechs verschiedenen Karpfenteichen. *Verh. int. Ver. Limnol.* 14: 700—708.

SMHI (Swedish Meteorological and Hydrological Institute), 1959—1962. Årsbok 41—44: I. Stockholm.

ŠRÁMEK-HUŠEK, R., 1962. Die mitteleuropäischen Cladoceren- und Copepodengemeinschaften und deren Verbreitung in den Gewässern der ČSSR. *Sci. P. Inst. Chem. Technol., Prague. Technol. of water 6 (7): 99—133.*

STRAŠKRABA, M., 1963. Share of the littoral region in the productivity of two fishponds in southern Bohemia. *Rozpravy Československé Akademie Věd, Ročník 73 — Sešit 13.*

THIENEMANN, A., 1926. *Holopedium gibberum* in Holstein. *Z. Morphol. Ökol. Tiere 5 (4): 755—776.*

TONOLLI, V., 1958, Zooplankton swarms. *Verh. int. Ver. Limnol. 13: 776—777.*

WALTER, E., 1934. Grundlagen der allgemeinen fischereilichen Produktionslehre einschliesslich ihrer Anwendung auf die Fütterung. Handb. Binnenfischerei Mitteleuropas 4: 5.

WEIMANN, R., 1942. Zur Gliederung und Dynamik der Flachgewässer. *Arch. f. Hydrob. 38: 481—524.*

WESENBERG-LUND, C., 1952. De danske søers og dammes dyriske plankton. København.

VOIGT, M., 1957. Rotatoria. Die Rädertiere Mitteleuropas. Berlin-Nikolassee.

WUNDER, W., 1935. Die Planktonröhre aus Cellhorn, ein neues hydrobiologisches Gerät. *Arch. f. Hydrob. 28: 659—662.*

Reports from the Institute of Freshwater Research, Drottningholm

*1. *Gunnar Alm.* Statens undersöknings- och försöksanstalt för sötvattensfisket. Dess tillkomst, utrustning och verksamhet. English summary. 1933. Pris kr. 0: 75.
*2. *Gunnar Alm.* Vätterns röding, Fiskeribiologiska undersökningar. Deutsche Zusammenfassung. 1934. Pris kr. 0: 75.
*3. *Christian Hessle.* Märkningsförsök med gädda i Östergötlands skärgård åren 1928 och 1930. English summary. 1934. Pris kr. 0: 50.
4. *Gottfrid Arvidsson.* Märkning av laxöring i Vättern. Deutsche Zusammenfassung. 1935. Pris kr. 0: 75.
*5. *Sten Vallin.* Cellulosafabrikerna och fisket. Experimentella undersökningar. Deutsche Zusammenfassung. 1935. Pris kr. 0: 75.
6. *Gunnar Alm.* Plötsliga temperaturväxlingars inverkan på fiskar. Deutsche Zusammenfassung. 1935. Pris kr. 0: 75.
*7. *Christian Hessle.* Gotlands havslaxöring. English summary. 1935. Pris kr. 0: 75.
8. *Orvar Nybelin.* Untersuchungen über den bei Fischen krankheitserregenden Spaltpilz Vibrio Anguillarum. 1935. Pris kr. 1: 25.
9. *Orvar Nybelin.* Untersuchungen über die Ursache der in Schweden gegenwärtig [illegible]kommenden Krebspest. 1936. Pris kr. 0: 75.
10. *E. Rennerfelt.* Untersuchungen über die Entwicklung und Biologie des Krebspestpilzes Aphanomyces astaci. 1936. Pris kr. 0: 75.
11. *Gunnar Alm.* Huvudresultaten av fiskeribokföringsverksamheten. Deutsche Zusammenfassung. 1936. Pris kr. 1: —.
12. *Gunnar Alm.* Industriens fiskeavgifter och deras användning. 1936. Pris kr. 1: 50.
13. *H. Bergström* och *Sten Vallin.* Vattenförorening genom avloppsvattnet från sulfatcellulosafabriker. 1937. Pris kr. 0: 75.
14. *Gunnar Alm.* Laxynglets tillväxt i tråg och dammar. English summary. 1937. Pris kr. 0: 75.
15. *Gunnar Alm.* Undersökningar över tillväxt m.m. hos olika laxöringformer. English summary. 1939. Pris kr. 2: 50.
16. *Lars Brundin.* Resultaten av under perioden 1917—1935 gjorda fiskinplanteringar i svenska sjöar. Deutsche Zusammenfassung. 1939. Pris kr. 1: —.
17. *Nils Törnquist.* Märkning av vänerlax. English summary. 1940. Pris kr. 1: —.
18. *Sven Runnström.* Vänerlaxens ålder och tillväxt. English summary. 1940. Pris kr. 1: —.
19. *Arne Lindroth.* Undersökningar över befruktnings- och utvecklingsförhållanden hos lax (Salmo salar). Deutsche Zusammenfassung. 1942. Pris kr. 0: 75.
*20. *Lars Brundin.* Zur Limnologie jämtländischer Seen. 1942. Pris kr. 2: —.
*21. *Gunnar Svärdson,* Studien über den Zusammenhang zwischen Geschlechtsreife und Wachstum bei Lebistes. 1943. Pris kr. 1: —.
*22. *Gunnar Alm.* Befruktningsförsök med laxungar samt laxens biologi före utvandringen. (Fertilization-Experiments with Salmon-parr.) English summary. 1943. Pris kr. 1: 50.

23. *Gunnar Svärdson.* Chromosome Studies on Salmonidae. 1945. Pris kr. 3: —.

24. *Arne Lindroth.* Zur Biologie der Befruchtung und Entwicklung beim Hecht. (Gäddans befruktnings- och utvecklingsbiologi samt gäddkläckning i glas.) 1946. Pris kr. 3: —.

25. *Gunnar Alm.* Reasons for the occurrence of stunted fish populations. (Uppkomsten av småväxta fiskbestånd, spec. hos abborre.) 1946. Pris kr. 3: —.

26. *Gösta Högström.* Olika impregneringsämnens lämplighet för grovgarnig fiskredskap. Deutsche Zusammenfassung. 1947. Pris kr. 1: —.

27. *A. Määr.* Über die Aalwanderung im Baltischen Meer auf Grund der Wanderaalmarkierungsversuche im finnischen und livischen Meerbusen i. d. J. 1937—1939. 1947. Pris kr. 2: —.

28. *Elias Dahr.* Biologiska studier över siken vid mellansvenska östersjökusten. English summary. 1947. Pris kr. 2: —.

29. Annual Report for the Year 1948 and Short Papers. 1949. Pris kr. 3: 50.

30. *Lars Brundin.* Chironomiden und andere Bodentiere der südschwedischen Urgebirgsseen. English summary. 1949. Pris kr. 15: —.

31. Annual Report for the Year 1949 and Short Papers. 1950. Pris kr. 3: 50.

32. Annual Report for the Year 1950 and Short Papers. 1951. Pris kr. 4: 50.

33. Annual Report for the Year 1951 and Short Papers. 1952. Pris kr. 8: —.

34. Annual Report for the Year 1952 and Short Papers. 1953. Pris kr. 8: —.

35. Annual Report for the Year 1953 and Short Papers. 1954. Pris kr. 8: —.

36. Annual Report for the Year 1954 and Short Papers. 1955. Pris kr. 8: —.

37. Report from the Institute of Freshwater Research, Drottningholm. 1956. Pris kr. 8: —.

38. Report from the Institute of Freshwater Research, Drottningholm. 1957. Pris kr. 8: —.

39. Report from the Institute of Freshwater Research, Drottningholm. 1958. Pris kr. 8: —.

40. Report from the Institute of Freshwater Research, Drottningholm. 1959. Pris kr. 8: —.

41. Report from the Institute of Freshwater Research, Drottningholm. 1960. Pris kr. 8: —.

42. Report from the Institute of Freshwater Research, Drottningholm. 1961. Pris kr. 8: —.

43. *Lars B. Höglund.* The Reactions of Fish in Concentration Gradients. 1961. Pris kr. 8: —.

44. Report from the Institute of Freshwater Research, Drottningholm. 1962. Pris kr. 8: —.

45. Report from the Institute of Freshwater Research, Drottningholm. 1964. Pris kr. 8: —.

46. Report from the Institute of Freshwater Research, Drottningholm. 1965. Pris kr. 12: —.

---

* Out of print.