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FISHERY BOARD OF SWEDEN

Nils Rosen

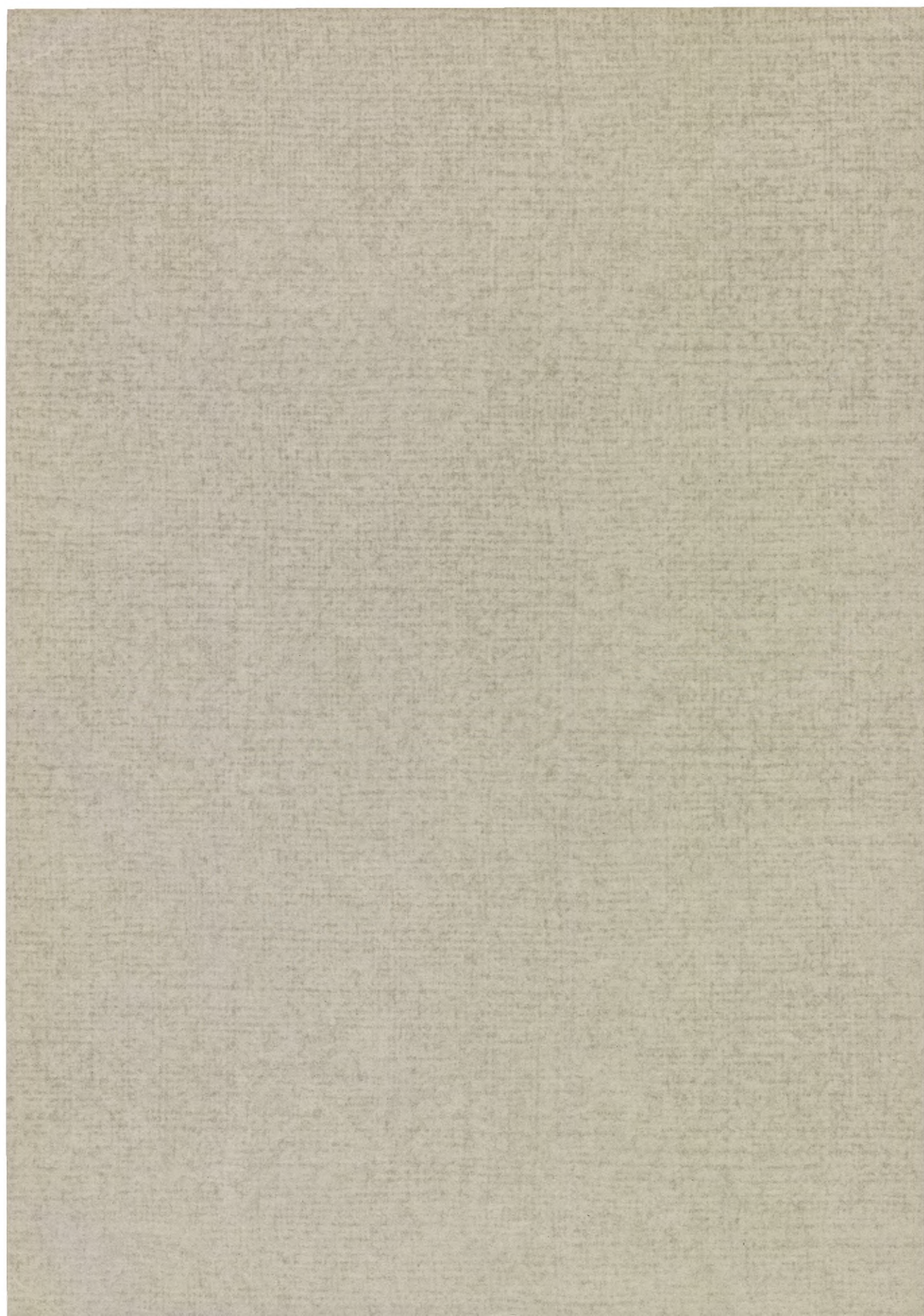
INSTITUTE OF FRESHWATER RESEARCH

DROTTHINGHOLM

Report No 42

LUND 1961

CARL BLOMS BOKTRYCKERI A.-B.



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Die Ergebnisse der Fischaussätze in den Kälarne-Seen

Von GUNNAR ALM

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I. Einleitung

An der Fischereiversuchsstation Kälarne, im östl. Teil der Provinz Jämtland auf dem 63. nördl. Breitengrad, in der norrländischen Nadelwaldregion belegen, wurden Versuche in das Arbeitsprogram aufgenommen, die im nördl. Schweden so gewöhnlichen sehr kleinen Seen fischökonomisch auszunützen. Es wurden Versuche geplant, die teils gewisse allgemeine limnologische Untersuchungen solcher in der Umgebung belegener Seen, teils das Aussetzen von Fischen verschiedener Art in denselben, umfassen sollten. Am Anfang galt es besonders Seen, wo Fische früher nicht vorgekommen waren, doch wurde allmählich auch eine Anzahl fischführender Seen in das Arbeitsprogramm mit einbezogen. In einem im Jahre 1960 von mir publizierten ersten Bericht über diese Wirksamkeit, wurden die verschiedenen Seen aus limnologischen Gesichtspunkten wie auch, mit Rücksicht auf die zu jener Zeit (Mitte 1930) damals vorhandenen Fischarten behandelt. Auch die Ursache zu den vielen fischleeren Seen wurden in diesem Zusammenhang diskutiert. Zu näherer Kenntnissnahme sei der Leser auf diesen Bericht verwiesen. In demselben wird auch eine Erklärung zur Nummerierung der Seen gege-

ben, ausserdem wird deren Einteilung in verschiedene Gruppen eingehend behandelt.

In dem nun vorliegenden Teil werden die Fischaussätze und deren Resultate behandelt. Die Absicht war wie schon oben bemerkt, zu erforschen inwiefern die hier in Frage kommenden vorzugsweise fischleeren Kleinseen ausgenützt werden könnten. Es gilt also zu erfahren, welche Faktoren die so wechselnden Resultate der Aussätze bewirkten, welcher Fischertrag erhalten werden kann aus diesen Kleinseen, und welche Bedeutung diesen vom Gesichtspunkt der Hausbedarf- und der Sportfischerei zugemessen werden kann. Für die Berufsfischerei sind solche Seen selbstverständlich wertlos. Auch soll daran erinnert werden, dass, als diese Versuche in Gang gekommen waren, die nun modernen Rotenonbehandlungen von Seen mit wertlosem Fischbestand, noch unbekannt waren.

Die Fischaussätze umfassten eine grosse Anzahl von Arten, sowohl Brut als auch in den Teichen der Versuchsstation aufgezogenen Fingerlingen und grösseren Jungen. Im letzteren Fall wurden zuweilen die Aussätze auf Grund von Transportschwierigkeiten in verhältnismässig leicht zugänglichen Seen gemacht, die vielleicht nicht immer die geeignetsten waren, und die ursprünglich nicht in das Aussatzprogramm des Jahres eingerechnet waren. Diese Aussätze, bei denen es sich meist um eine kleinere Anzahl Fische drehte, sind trotzdem mitbehandelt worden. Dagegen wurden nicht berücksichtigt gewisse Aussätze von Fischen, die in respektiven Seen schon vorher vorhanden waren. In einigen Fällen erfolgten Aussätze in Seen, die nicht Gegenstand limnologischer Untersuchungen waren. In den letzten Jahrzehnten wurden teilweise auch von der dort lebenden Bevölkerung Aussätze gemacht. Soweit bekannt, sind diese mitbehandelt worden. Verschiedentlich erfolgten Aussätze derselben Fischart zwei-, in anderen Fällen dreimal im selben See. Ausserdem wurden in vielen Seen Aussätze mehrerer Fischarten gemacht.

Die Genehmigung zu Aussätzen, sowie zu den unten berührten Probefängen, wurde durch Übereinkommen mit den teils privaten Fischwasserbesitzern, teils, soweit es Seen auf staatl. Boden betraf, mit dem Revierpersonal der Domänenverwaltung erhalten. Es muss auch hervorgehoben werden, dass eine Mehrzahl Aussätze verschiedener Coregonen-Formen im Zusammenhang mit SVÄRDSONS Untersuchungen (1950, 1952, 1953) über die Systematik der Coregonen, stattgefunden hat.

Um die Resultate der Aussätze erfahren zu können, wurden Probefänge gemacht. Diese wurden fast ausschliesslich auf den Spätsommer und den Herbst verlegt, wo der Zuwachs des Jahres im allgemeinen abgeschlossen war. Zu den Probefängen wurden Netze verschiedener Maschenweite angewandt, doch einigermassen angepasst an die zu erwartende Grösse der eingesetzten Fischarten. Oft wurden die Probefänge schon im Herbst des gleichen Jahres ausgeführt, in dem die Aussätze im Frühjahr gemacht worden

waren. In den meisten Fällen erfolgten Probefänge auch die nächstfolgenden Jahre hindurch. In gewissen Seen wurden diese über eine lange Folge von Jahren ausgedehnt.

Leider wurden in den Seen, in denen Aussätze gute Resultate gezeigt hatten, beweisbar Raubfang getrieben, und zwar oft in bedeutendem Ausmass. Dies war unmöglich zu verhindern, da die grösste Anzahl der Seen isoliert in oft weitgestreckten Waldbezirken liegt. Besonders wurden Forelle und Saibling, die durch Springen und Ringbildungen auf der Wasserfläche ihre Anwesenheit verraten, Gegenstand des Raubfanges. In vielen Fällen wurden von den Raubfischern extra Flotten gebaut, um Netze und Angelgeräte anwenden zu können. Auf diese Weise konnten auch Felchen bequem gefangen werden. Die durch die Versuchsstation erhaltenen Resultate sind daher oft zu nieder. Sicher ist, dass in mehreren Fällen ausgebliebene oder besonders schlechte Probefänge auf diesem Raubfang beruhen.

Wie schon genannt, galten die Aussätze hauptsächlich den Kleinseen, die meisten nur von einigen Hektars. Oft waren Ufer und Böden lose, moorig und schlammig, weshalb man nicht damit rechnen konnte dass die ausgesetzten Fischarten sich fortpflanzen und feste Bestände bilden könnten. Welchen direkten Wiederfang man erhalten könnte, war die Hauptsache zu erfahren. Zuweilen wurden Aussätze auch in grösseren Seen gemacht. Selbstverständlich was es schwer an Hand einzelner Probefänge eine Auffassung zu gewinnen über das Resultat derselben. Es konnte geschehen, dass von der ausgesetzten Fischart nicht ein einziger Wiederfang gemacht werden konnte.

In einer Zusammenstellung wie der vorliegenden, wäre eine detaillierte Angabe über jeden einzelnen Aussatz unnötig belastend gewesen. Dagegen wurde eine allgemeine Übersicht über sämtlich gemachten Aussätze in Tabellenform aufgestellt. In weiteren Zusammenstellungen, ebenfalls in Tabellenform, sind die Anzahl Aussätze der verschiedenen Fischarten, die Aussätze mit Berücksichtigung der Brut, einjähriger Exemplare usw., aufgeführt.

In einer der folgenden Kapitel wird zuerst ein allgemeiner Überblick gegeben über die Resultate der Aussätze, darauf wird jede Fischart für sich behandelt. Aussätze, die keine oder nur sehr geringe Wiederfänge ergeben haben, werden mehr summarisch, doch mit besonderer Beachtung der speziell hereinspielenden Faktoren behandelt. Aussätze mit guten Resultaten werden dagegen eingehender behandelt. Da genaue Angaben über die Resultate solcher Fischaussätze selten sind, schien es mir von Interesse, da solche Angaben nun vorliegen, eine Mehrzahl davon in Tabellenform und als Diagramme mit hereinzunehmen.

In einem weiteren Kapitel werden diese Fragen mehr allgemein behandelt, auch wird der Fangertrag von anderen Seen der Kälarne-Umgebung berührt.

In dem oben genannten ersten Bericht dieser Untersuchungen der Kälarne-Seen, habe ich schon denen, die mir behilflich waren, meinen Dank vorgebracht. Doch will ich nicht versäumen, auch nun meinen warmen Dank an alle diejenigen Personen zu richten, die mir behilflich waren bei der Aussetzung der Fische und bei den Probefängen, besonders an den früheren und den jetzigen Vorsteher der Fischereiversuchsstation, dem Oberfischmeister G. MOLIN, und dem Fischmeister E. HALVARSSON.

II. Übersicht über die Seetypen und die Fischaussätze

In Tabelle 1 wird eine Übersicht über sämtliche Aussätze gegeben. Die Seen sind dort in dieselben Gruppen aufgenommen, in die sie schon früher, mit Rücksicht auf ihre limnologischen Eigenschaften, eingegliedert worden sind (vergl. Alm 1960 Tab. 3—6). Es wurde eine Mehrzahl von Faktoren die hier hereinspielen, in der Tabelle 1 aufgeführt, in der Absicht, eine allgemeine Orientierung zu erleichtern, was die Typen der Seen betrifft. Hierzu muss bemerkt werden, dass die Transparenz-Verhältnisse als Grund dieser Einteilung in Gruppen verwendet wurde. Zu Gruppe I wurden Seen mit einer Transparenz von höchstens 2,0 m, zu Gruppe II eine Transparenz von 2,1—3,0 m, zu Gruppe III eine Transparenz von 3,1—5,0 m und zu Gruppe IV schliesslich Seen mit einer Transparenz von über 5 m gerechnet.

Aus Tabelle 1 geht weiter hervor, dass sich die vier Gruppen auch in anderer Hinsicht wesentlich unterscheiden, nämlich dass von Gruppe I bis IV die Seefarbe allmählich von dunkelbraunen zu hellgrünen Tönen übergeht, und PH, Alkalinität ($\text{cm}^3 \text{ n}/10 \text{ HCl pro } 100 \text{ cm}^3$) und Leitvermögen ($\text{K}_{20} \cdot 10^6$) von niederen zu höheren Werten. Aus Teil I kann ausserdem entnommen werden, wie die O_2 -Verhältnisse, die in Gruppe I oft sehr ungünstig sind, sich im grossen und ganzen allmählich verbessern, je mehr wir uns den Seen der Gruppen III und IV nähern. Der Artreichtum der Vegetation nimmt ebenfalls zu, während Litoral- und Bodenfauna, abgesehen von gewissen Formen, keine grösseren Veränderungen eingeht. Die Anzahl der Fischarten nimmt innerhalb der Gruppeneinteilung I—IV zu, während die Zahl der fischleeren Seen abnimmt.

In derselben Tabelle wurden ausserdem Angaben gemacht über Fischarten, die schon vor 1930 vorgekommen sind, was ja in diesem Zusammenhang von speziellem Interesse ist. Auch von den Seen, die nicht Gegenstand limnologischer Untersuchungen waren, wurden solche Angaben gesammelt. Hinsichtlich dieser Verhältnisse soll hier bemerkt werden, dass zwei in Tabelle 27 des ersten Berichts 1960 aufgenommenen Seen, bei näherer Nachforschung Fischarten gezeigt haben, welche früher von den Bewohnern der Gegend ausgesetzt worden sind. Dies betrifft den in dieser Tabelle genannten und als fischleer aufgenommenen Lejonrostjärn, C 205, in den mit gutem Resultat

Tabelle 2. Zahl der Aussätze der verschiedenen Fische.

Fisch	Gruppe					Sämtl.
	I	II	III	IV	? ¹	
Lachs	2	1	1	—	—	4
Lachs×Forelle	2	—	1	—	1	4
Bachforelle	12	12	3	2	1	30
Seeforelle	8	7	3	2	4	24
Meerforelle	4	6	—	1	—	11
Forellen-Kreuzungen	—	1	1	1	—	3
Regenbogenforelle	2	1	—	1	1	5
Saibling	3	1	2	2	—	8
Bachsaiibling	6	2	5	1	—	14
Saibling×Forelle	2	—	1	—	1	4
Saibling×Bachsaiibl.	1	2	4	2	1	10
Äsche	1	1	1	—	—	3
Coregonen, verschiedene Arten	13	16	12	2	1	44
Coregonen-Kreuzungen	5	—	—	—	2	7
Kleine Maräne	—	1	—	—	—	1
Grosse×Kleine Maräne	2	1	1	—	4	8
Barsch	3	4	—	—	—	7
Zander	—	—	3	—	—	3
Hecht	1	2	1	—	—	4
Aal	2	3	3	—	—	8
Übrige	2	2	1	—	—	5
Sämtl.	71	63	43	14	16	207
%	34,3	30,4	20,8	6,8	7,7	

¹ Nicht näher untersucht.

etwa zu Beginn des Jahrhunderts und auch verschiedene Male später Coregonen ausgesetzt worden waren. Was den Storörmyrtjärn C 160 mit der Angabe nur Saiblinge zu haben betrifft, wo aber der Saiblingbestand um das Jahr 1940 schon sehr stark zurückgegangen war, wurde etwa um das Jahr 1914 Barsch eingeführt.

Die Bezeichnungen 0, 1, und 2 in der Tabelle 1, die später näher besprochen werden sollen, (S. 13) geben an, dass die Resultate der Aussätze negativ (0), ziemlich schlecht (1), oder gut (2) waren. Sofern also, denselben See betreffend, die Ziffern 0 und 2 für eine gewisse Fischart angegeben sind, bedeutet das zwei Aussätze mit negativem bzw. gutem Resultat. In Tabelle 2 wurde eine übersichtliche Zusammenfassung der Tabelle 1 gemacht. Aus Fig. 1 geht die Lage der Seen innerhalb der Gebiete hervor, in die die limnologischen Untersuchungen verlegt waren. In Fig. 2 wurden sämtliche hier belegene Aussätzseen besonders markiert. Einige dieser Seen befinden sich allerdings ausserhalb dieses Gebietes.

Aus den beiden Tabellen geht somit hervor, dass Aussätze in insgesamt 92 Seen gemacht wurden, von denen 23 Gruppe I, 30 Gruppe II, 20 Gruppe III, 7 Gruppe IV und schliesslich 12 den nicht untersuchten Seen angehören. Auf grund mehrerer im gleichen See gemachten Aussätze, teils der gleichen

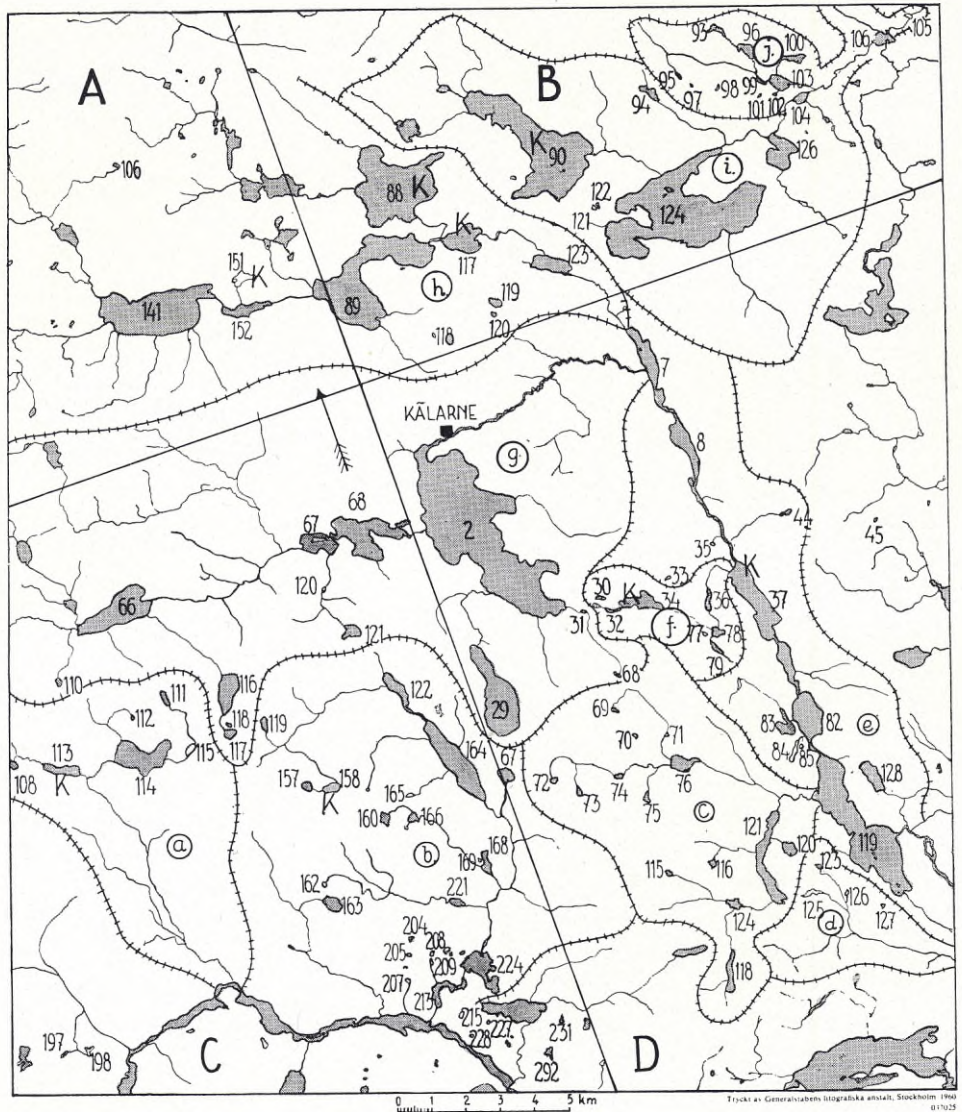


Fig. 1. Das engere Untersuchungs- und Fischeinsatzgebiet mit den nummerierten Seen. Die Buchstaben A—D entsprechen verschiedenen Kartenblättern, die Buchstaben a—j den kleineren Wassergebieten. K=Kalk-Vorkommen.

Art, teils verschiedener Arten, beträgt indessen die Anzahl der Aussätze 207 solche. Davon kommt die grösste Anzahl nämlich 71 oder 34,3 % auf die Seen der Gruppe I.

Die Forelle ist die Fischart die am meisten ausgesetzt wurde, mit insgesamt 68 Aussätzen der verschiedenen Formen, was 33 % aller Aussätze

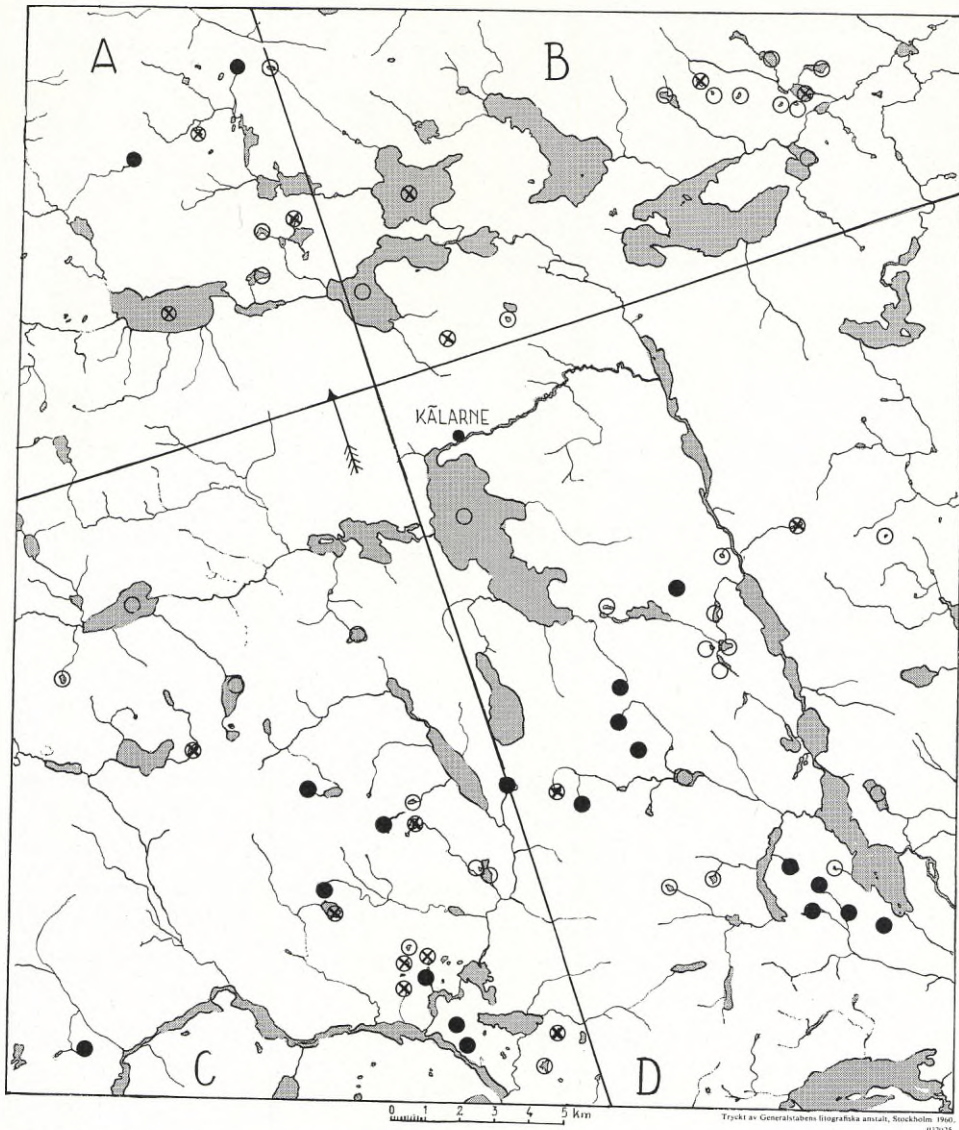


Fig. 2. Die Lage der Seen, in welchen die in der Tabelle 1 aufgenommenen Fischeaussätze gemacht sind. ●=Aussätze mit 2-Resultaten; ⊗=Aussätze mit 1-Resultaten; ○=Aussätze mit 0-Resultaten.

ausmacht. Dass die Forelle so stark dominiert, beruht hauptsächlich darauf, dass diese in eine Serie von Experimenten einging, Wachstumszunahme und andere Eigenschaften der Bach- und Seeforelle betreffend, die die Versuchstation in einem früheren Arbeitsprogramm ausgeführt hatte (ALM 1949, 1959). Ein reiches Material an Forellen zum Aussatz in verschiedenen Alters-

Tabelle 3. Alter der ausgesetzten Fische.

Fisch	Brut.	Alter in Sömmern oder Jahren					Sämtl.
		1	2	3	4	?	
Lachs	—	1	1	2	—	—	4
Lachs×Forelle	1	1	1	1	—	—	4
Bachforelle	12	8	5	2	—	3	30
Seeforelle	8	8	4	3	1	—	24
Meerforelle	3	5	1	—	2	—	11
Forellen-Kreuzungen	1	2	—	—	—	—	3
Regenbogenforelle	3	1	—	1	—	—	5
Saibling	2	6	—	—	—	—	8
Bachsaibling	—	11	—	1	1	1	14
Saibling×Forelle	4	—	—	—	—	—	4
Saibling×Bachsaibl.	6	1	—	3	—	—	10
Äsche	—	—	2	1	—	—	3
Coregonen, verschiedene Arten	29	4	3	2	3	3	44
Coregonen-Kreuzungen	7	—	—	—	—	—	7
Kleine Maräne	1	—	—	—	—	—	1
Grosse×Kleine Maräne	7	1	—	—	—	—	8
Barsch	1	1	—	—	—	5	7
Zander	—	3	—	—	—	—	3
Hecht	4	—	—	—	—	—	4
Aal	7	—	—	—	—	1	8
Übrige	—	—	—	—	—	5	5
Sämtl.	96	53	17	16	7	18	207
%	46,4	25,6	8,2	7,7	3,4	8,7	

stadien war somit von Anfang vorhanden. Auch war von grossem Interesse, mit Rücksicht auf die Sportfischerei, speziell die Möglichkeit Forellenbestände in den betreffenden Kleinseen erhalten zu können, zu erforschen.

Erst später wurden in grösserem Ausmass Versuche mit verschiedenen Coregonen eingeleitet. Insgesamt betragen diese Aussätze 60 oder 29 %. Saiblinge, Bachsaiblinge und Kreuzungen mit diesen Arten kommen danach mit etwa 17 %, während andere Fischarten erst viel später kommen, und nur einzelne Aussätze mit Zander, Kleine Maräne, Plötze, Karausche und Elritze geschahen.

Tabelle 3 gibt eine Übersicht über das Alter der Fische zur Zeit der Aussatzung. Nahezu die Hälfte aller Aussätze bzw. 46,4 % geschah mit Brut. Alle diese Brutaussätze erfolgten im Frühjahr. Einsömmerige und ältere Jungen wurden teils im Herbst teils im darauffolgenden Frühjahr eingesetzt. Diese sind doch in beiden Fällen als einjährige, zweijährige usw. Jungen bezeichnet worden. Bei gewissen Arten wie Saiblingkreuzungen und Coregonen, dominiert die Anwendung von Brut, während z.B. von See- und Meerforelle, Saibling und Bachsaibling einjährige und ältere Stadien meistens verwendet wurden. Dies hängt vor allem mit den oben genannten Experimenten zusammen. Mit Coregonen wurden solche Versuche nicht in derselben Umfang gemacht.

III. Resultate der Aussätze

1. Allgemeine Übersicht

Aus Tabelle 1 geht wie schon oben berührt, das Resultat eines jeden Aussatzes hervor. Bei der Beurteilung derselben wurde gewisse Rücksicht genommen auf Art und Grösse des Fisches. Vom Gesichtspunkt der Sportfischerei gesehen, ist z.B. eine Anzahl wiedergefangener Forellen selbstverständlich von grösserem Wert, als dieselbe Anzahl Coregonen, was auch von Fischen die nicht so gross sind gilt. Was die Lachsfische betrifft, wurden deshalb Wiederfänge von z.B. 17, 18, 20 Fischen als gut bezeichnet. Bei Coregonen-Aussätzen dagegen war es selten, dass nur 25—30 Wiederfänge gemacht wurden, meist waren es wenigstens 50 und in vielen Fällen bis zu 100 Exemplare. Diese unterschiedlichen Resultate beruhen sicher hauptsächlich auf Raubfischerei, die grösseren Wert auf Lachsfische als auf Coregonen legt, und dadurch die Möglichkeit grössere Wiederfänge der ersteren zu erreichen vermindert. Aus den angeführten Gründen schien es geeignet, ganz abgesehen vom Raubfang, die Resultate in drei Gruppen 0, 1, und 2 einzuteilen. Zu Gruppe 0 sind solche Aussätze gerechnet worden, die 0—5 Wiederfänge ergaben. Gruppe 1 umfasst Aussätze mit einem Wiederfang von 6—15 Exemplaren, was im allgemeinen als ein ziemlich schlechtes oder mittelmässiges Resultat bezeichnet werden muss. Zu Gruppe 2 wurden Wiederfänge von mindestens 16 Fischen gerechnet. Angaben über Aussätze mit 2-Resultaten wurde für jede Art in besonderen Tabellen zusammen geführt. Auf diese Weise bekommt man einen besseren Überblick über den Ertrag solcher Kleinseen, wie auch über die Gestaltung des Wachstums und der Grössengruppierung innerhalb einer bestimmten Alter.

Für diese Tabellen gilt folgendes: Die Seen sind, jede Fischart betreffend, in dieselbe Ordnung eingeteilt wie in Tabelle 1. Im Anschluss an den Namen des Sees, findet man die Angaben über die Aussätze. „F 36-2-150“ bedeutet z.B. Frühling 1936, zweijährige Exemplare, 150 Stück, „H 51“=Herbst 1951, „S 42“=Sommer 1942, usw. Die übrigen Spalten geben Fangjahr, und wenn nichts anderes genannt wird, immer die Herbstzeit betreffend, die Anzahl gefangener Exemplare, deren Alter, Gewicht und Länge an. In mehreren Tabellen befindet sich eine Spalte „gefangen und zurückgesetzt“. In der Absicht so viel Fische als möglich zwecks Zuwachs und für den Fang folgender Jahre zu sparen; wurde hier und da eine Anzahl von unbeschädigten Exemplaren nach genauen Messungen zurückgesetzt. Diese sind nicht in der Spalte „sämtliche“ und auch nicht in den Gewichtsziffern mitgerechnet. Die Längenziffern dagegen umfassen auch diese Exemplare. Nur in Fällen in denen im darauffolgenden Jahr keine Wiederfänge gemacht wurden, wurden die ausgesetzten Exemplare als gefangen angesehen und folglich in die Spalte „sämtliche“ aufgenommen. Fangjahre die keinen Fang zu verzeichnen

hatten, sind nicht mitgerechnet, auch nicht die Jahre in denen keine Probenfänge gemacht wurden.

Was die Spalten für männliche und weibliche Exemplare betrifft, bezeichnen die dort aufgenommenen Ziffern dass die entsprechende Anzahl Exemplare reif waren, und zwar meist während oder kurz vor der Laichzeit, manchmal auch ausgelaichte solche. Wenn diese Ziffern nicht mit denen unter „sämtliche“ übereinstimmen, so bedeutet das, dass die übrigen Exemplare juvenil waren. Wo Ziffern fehlen, wurden keine Untersuchungen über Geschlecht und Reife gemacht. Zuweilen waren alle Exemplare reif, ohne dass die Anzahl beider Geschlechter vermerkt wurde. Die Gewichtsziffern basieren meist auf tatsächlichen Ergebnissen, zuweilen doch berechnet auf grund vorliegender Ziffern andrer Jahre.

2. Die verschiedenen Fischarten

Im Folgenden werden die Resultate jeder einzelnen Fischart behandelt, unter Hinweis auf Tabelle 1.

Lachs (*Salmo salar* L) und Kreuzungen Lachs×Forelle (*Salmo trutta*)

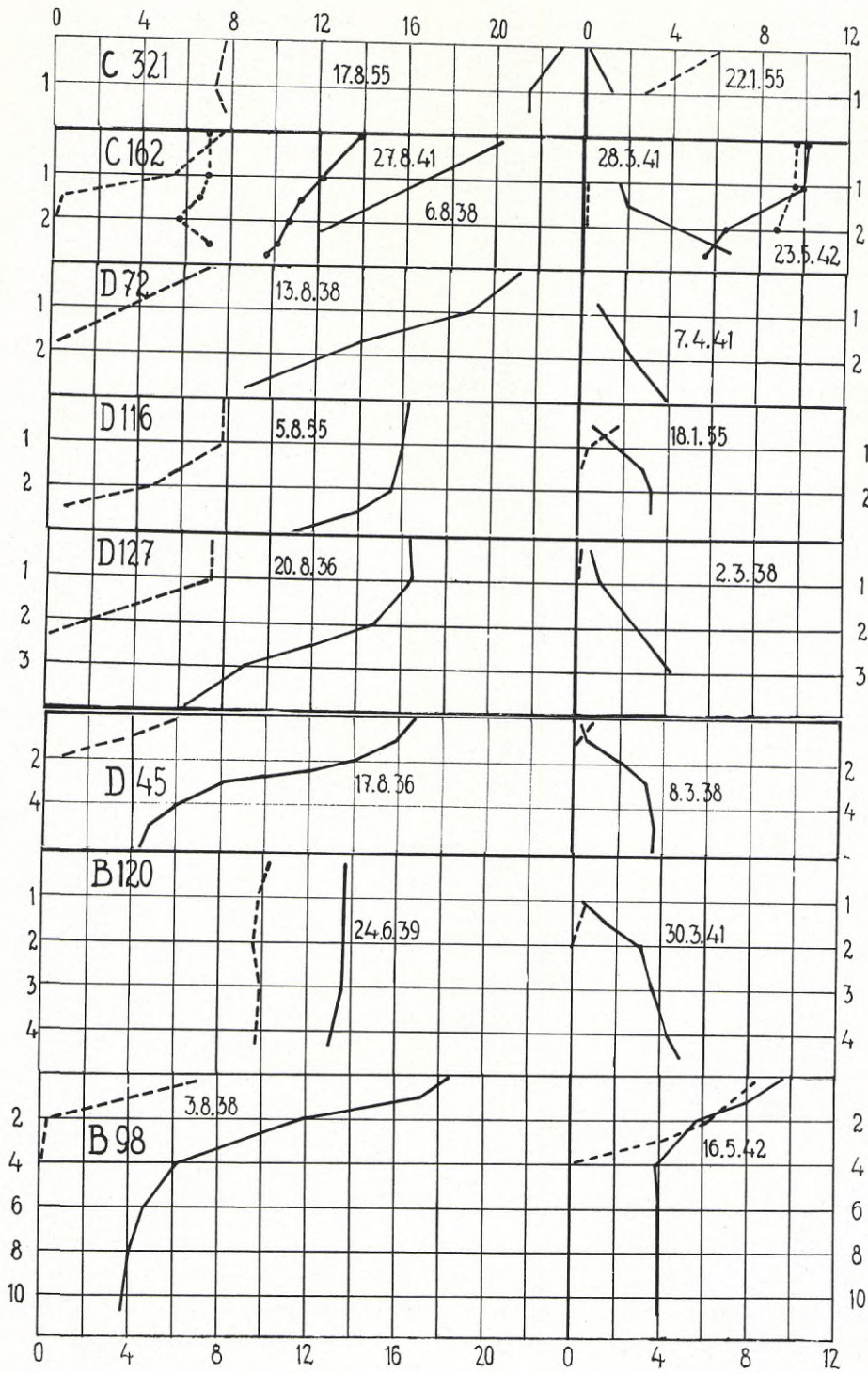
Lachs wurde in 4 Seen ausgesetzt: Grästjärn D 69, Långtjärn B 95, Libergstjärn C 228, och Myrbärtjärn C 165 mit respektive 500 einjährigen, 120 dreijährigen, 290 zweijährigen und 30 dreijährigen Exemplaren. In den drei letztgenannten Seen befanden sich früher Barsche, im Grästjärn früher mit gutem Erfolg ausgesetzte Forellen und Saiblinge. Trotzdem die ausgesetzten Lachsungen eine Grösse von ungefähr 5—8 cm (1 Jahr) 7—13 cm (2 Jahr) und 10—22 cm (3 Jahr) gehabt haben, wurden nur respektive 7, 6, 11, und 3 Exemplare in diesen 4 Seen wiedergefangen. Vermutlich war Nahrungskonkurrenz und Auswanderung (nur der Libergtjärn C 228 vermisst Ablauf) die wahre Ursache zu diesen spärlichen Wiederfängen. Sicher hat auch die geringe Grösse der Seen die Auswanderung beschleunigt. Der grösste wiedergefangene Lachs (ausgesetzt als einjährig) erreichte eine Länge von 37 cm innerhalb einer Zeit von zwei Jahren.

Die Ursachen zu diesen schlechten Resultaten der Lachsaussätze, das Vorkommen von Konkurrenten und Auswanderung, sind sicher auch zu-

Fig. 3. Beispiele der Temp.- und O₂-Verhältnisse in Seen, die im Winter meistens totalen O₂-Mangel haben.

C 321 Lilltjärn x; C 162 La Holmtjärn x; D 72 V. Vontjärn x; D 116 Klingertjärn x; D 127 Lugnsjötjärn x; D 45 Skimsåstjärn x; B 120 La Meckflotjärn B; B 98 Bytjärn x.
x = vom Anfang fischleer, übrige Bezeichnungen siehe die Erklärung zur Tab. 1.

In diesen und den Figuren 4—7 sind die Temp.-Kurven liniert, die O₂-Kurven gestrichelt. Wenn mehrmals untersucht, sind die Kurven verschieden ausgestaltet.



treffend bei den vier Aussätzen von Lachs×Forelle (Brut und ein- bis zweijährige Jungen) welche vollständig negativ ausfielen. Es soll auch daran erinnert werden, dass die Verluste solcher Kreuzungen durchweg grösser sind als bei den Eltern (Alm 1955).

Sämtliche nun berührte Seen, in die Lachs und Lachsforelle ausgesetzt wurden, gehören zu den kleinsten Seen von nur 1—2,5 ha, ausser Krängtjärn D 78 von 7 ha, in dem ausser Barsch auch Hecht vorkommt.

Bachforelle (*Salmo trutta fario* L)

Von 30 Aussätzen der Bachforelle ergaben 20 0-Resultate. Dies gilt sämtliche Aussätze von Brut und die Mehrzahl einjähriger Jungen. Die halbe Anzahl dieser Seen hatten Barsch, zuweilen auch Hecht, weshalb die Aussichten geglückte Resultate zu erhalten sehr klein waren. Was die übrigen zehn ursprünglich fischleeren Seen mit 0-Resultat betrifft, wurden früher mit gutem Resultat in drei dieser Seen, Ö. Vontjärn D 73, Ilvåstjärn D 33 und V. Rörtjärn C 157, ältere Bach- und Seeforellen resp. Coregonen und Saiblinge ausgesetzt. Es ist anzunehmen, dass diese die neuausgesetzten Brut sowie die kleinen einjährigen Bachforellen gefressen bzw. ausgeschlagen haben. In zwei Seen mit Elritze, dem Stockbergjärn A 106 und dem Mantjärn C 152, im letzteren auch Plötze, wurden 21 resp. 10 Wiederfänge erhalten, in beiden Fällen mit einer grössten Länge von 36 cm (siehe Tab. 4). Die gleiche Tabelle zeigt, dass von einjährigen Bachforellen, ausgesetzt in dem fischleeren Grästjärn D 69, 28 Ex. wiedergefangen wurden, mit einer grössten Länge von 40 cm.

Was die übrigen fischleeren Seen betrifft, wurden im V Vontjärn D 72 im Herbst desselben Jahres in dem die Aussätze geschehen waren 1 resp. 5 ein-sommerige Bachforellen mit einer ungefährlichen Länge von 9—10 cm erhalten, dagegen keine im Jahr darauf. Totaler O₂-Mangel während des Winters hat offenbar den Tod der übrigen bewirkt. Fig. 3 zeigt die Temperatur- und O₂-Verhältnisse in einigen Aussätzseen mit jährlichen O₂-Mangel. Man kann mit Sicherheit davon ausgehen, dass dieser Faktor auch in gewissen anderen von Anfang an fischleeren Seen die negativen Resultate verursacht hat, wo sonst Aussätze von Brut günstige Voraussetzungen gehabt haben, z.B. Lugnsjötjärn D 127 und Skimsåstjärn D 45, welche beide bei den Untersuchungen im März 1938 nahezu totalen O₂-Mangel zeigten. In Fig. 4 sind Temperatur- und O₂-Kurven gewisser Aussätzseen eingetragen, wo die O₂-Verhältnisse im allgemeinen zu einem positiven Resultat kein Hindernis gewesen sein, wenn nicht totaler O₂-Mangel in gewissen Jahren mit kalten und langen Wintern eingetreten wäre, z.B. 1940—42 und 1954—55. Die O₂-Kurven im Winter 1941 haben nämlich vergl. mit anderen Wintern gezeigt, dass totaler O₂-Mangel vermutlich in diesem Jahr entstanden ist. Fig. 5—7 schliess-

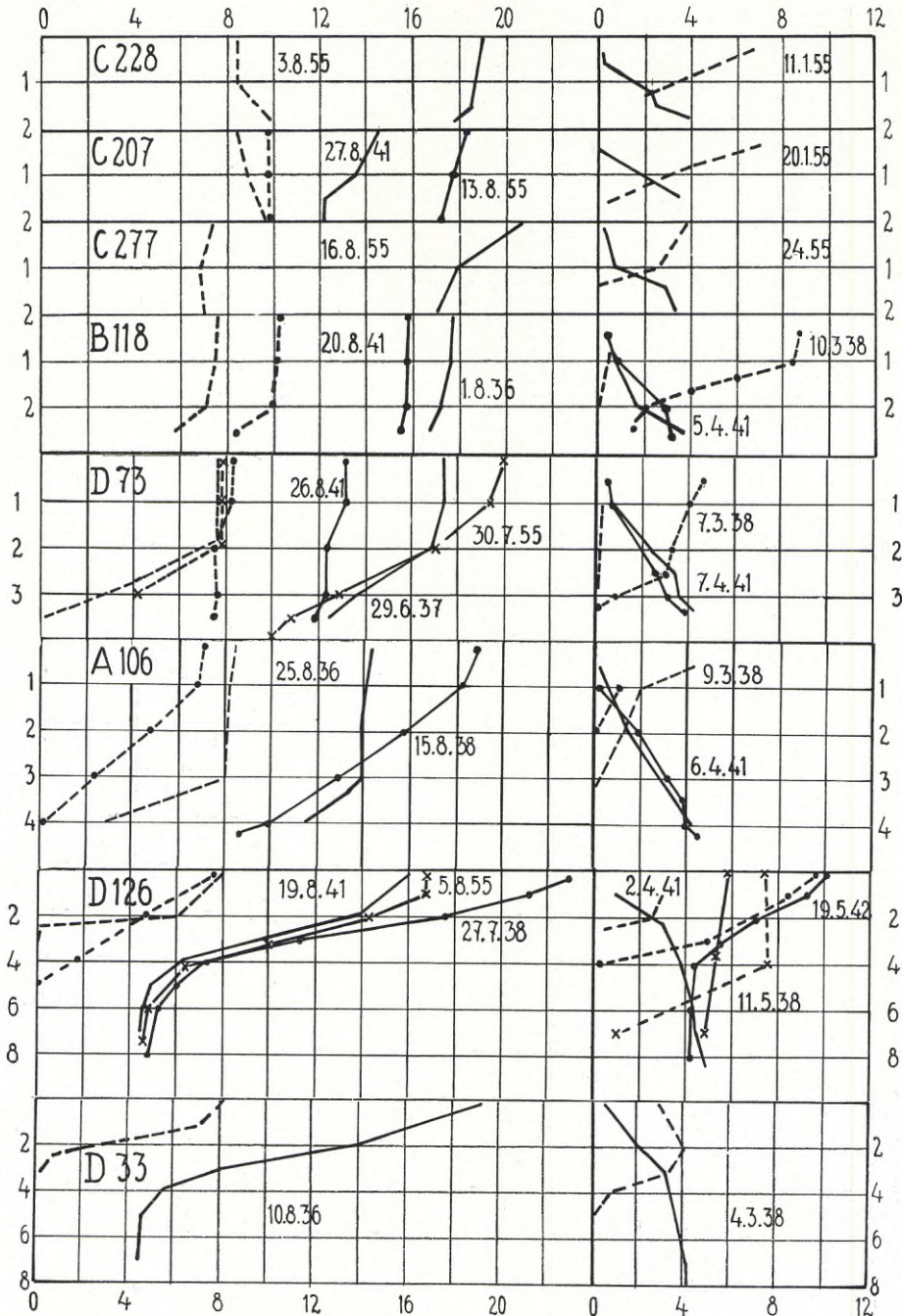


Fig. 4. Beispiele der Temp.- und O₂-Verhältnisse in Seen, die im Winter wahrscheinlich nur in einzelnen Jahren totalen O₂-Mangel haben.

C 228 Libergstjärn x, C 207 Kapelltjärn x; C 277 La Hälltjärn x; B 118 Barntjärn x, D 73 Ö. Vontjärn x; A 106 Stockbergstjärn, E.; D 126 Abborrtjärn 1, B.; D 33 Ilvästjärn x.

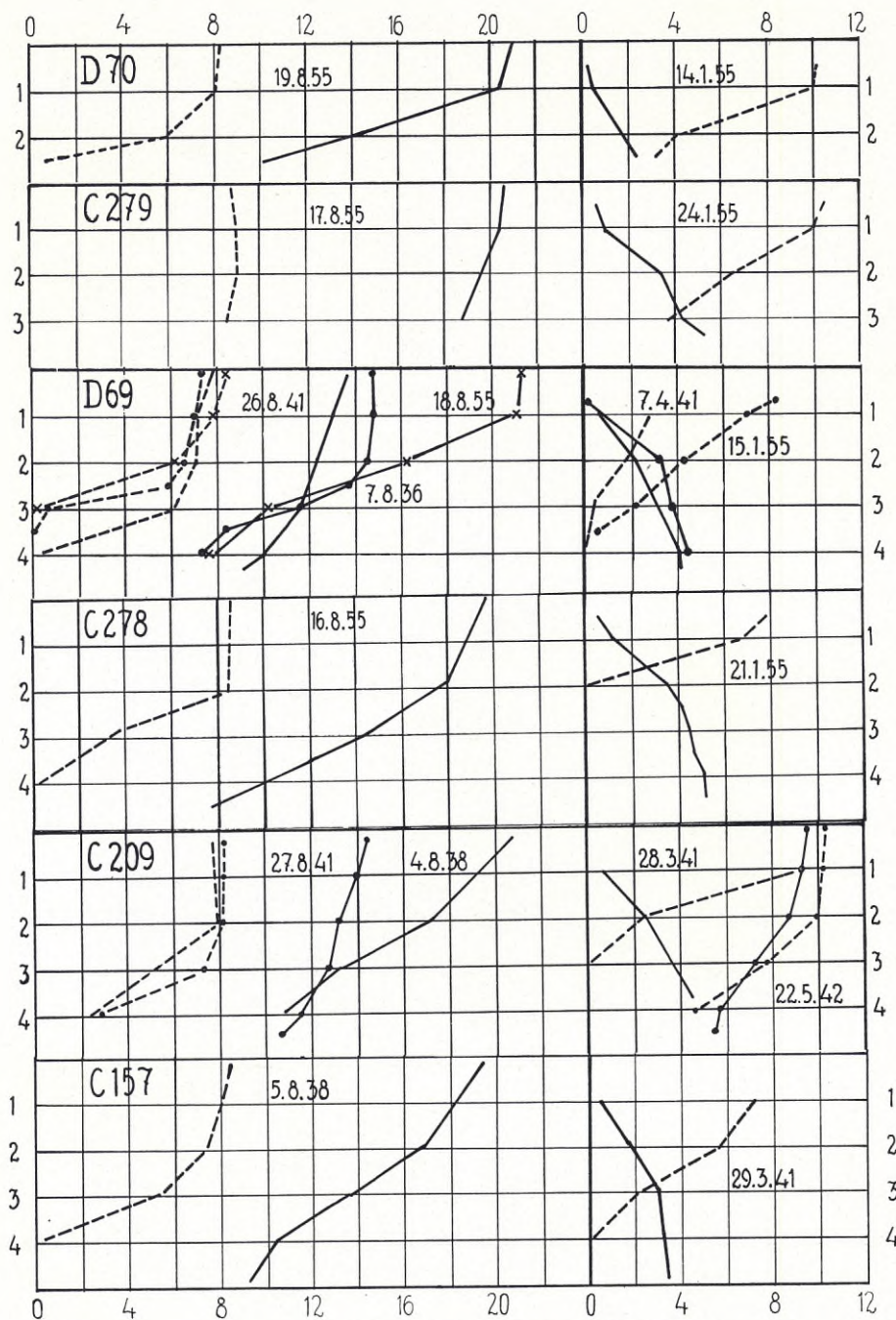


Fig. 5. *Beispiele der Temp.- und O₂-Verhältnisse in Seen die im Winter wahrscheinlich niemals totalen O₂-Mangel haben. Seen höchstens 5 m. tief.*

D 70 Hundtjärn x; C 279 Svarttjärn x; D 69 Grästjärn x; C 278 St. Hälltjärn x; C 209 S. Kyrktjärn, B.; C 157 V. Rörtjärn x.

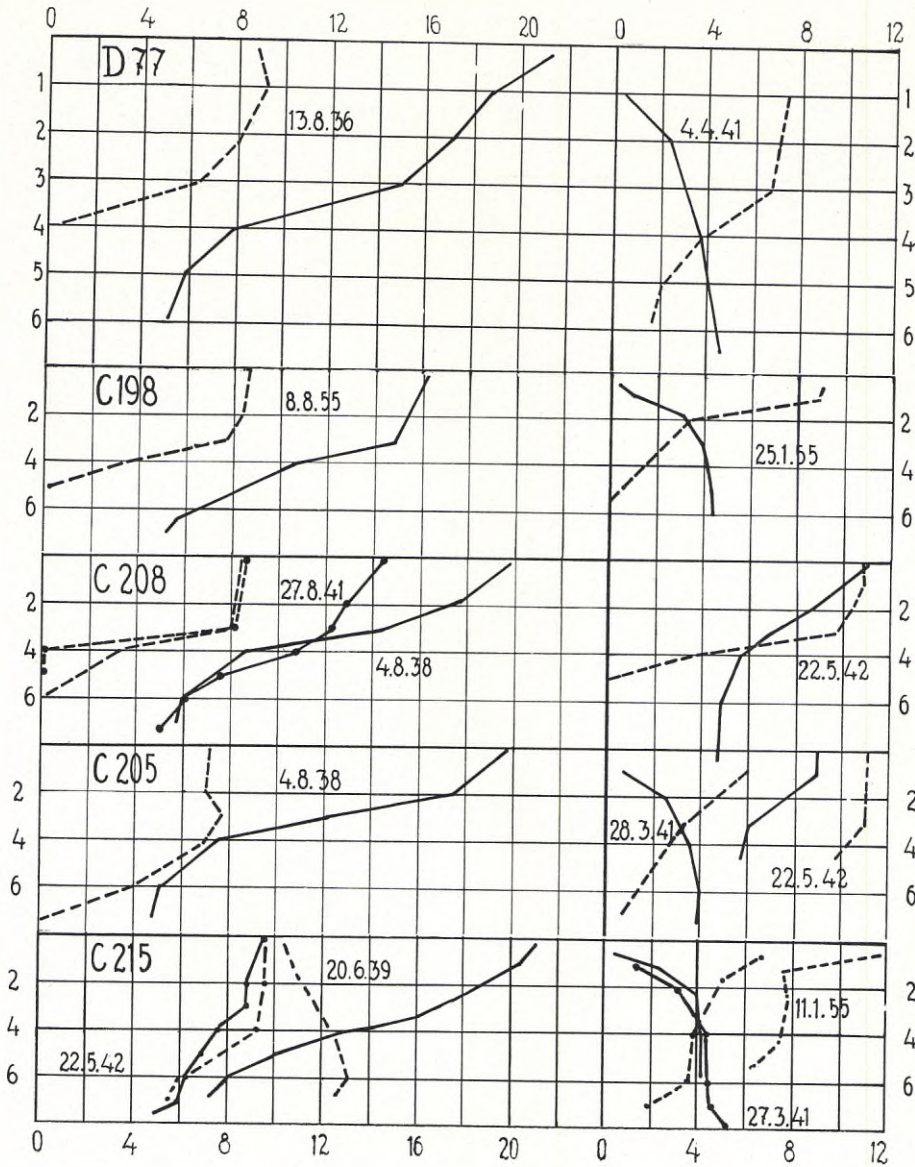


Fig. 6. Dasselbe wie in Fig. 5, aber Seen 6—7 m tief.

D 77 Abborrtjärn, B. H.P.; C 198 Ö. Gravtjärn x; C 208 N. Kyrktjärn B.; C 205 Lejonros-tjärn, C.; C 215 Nissetjärn x.

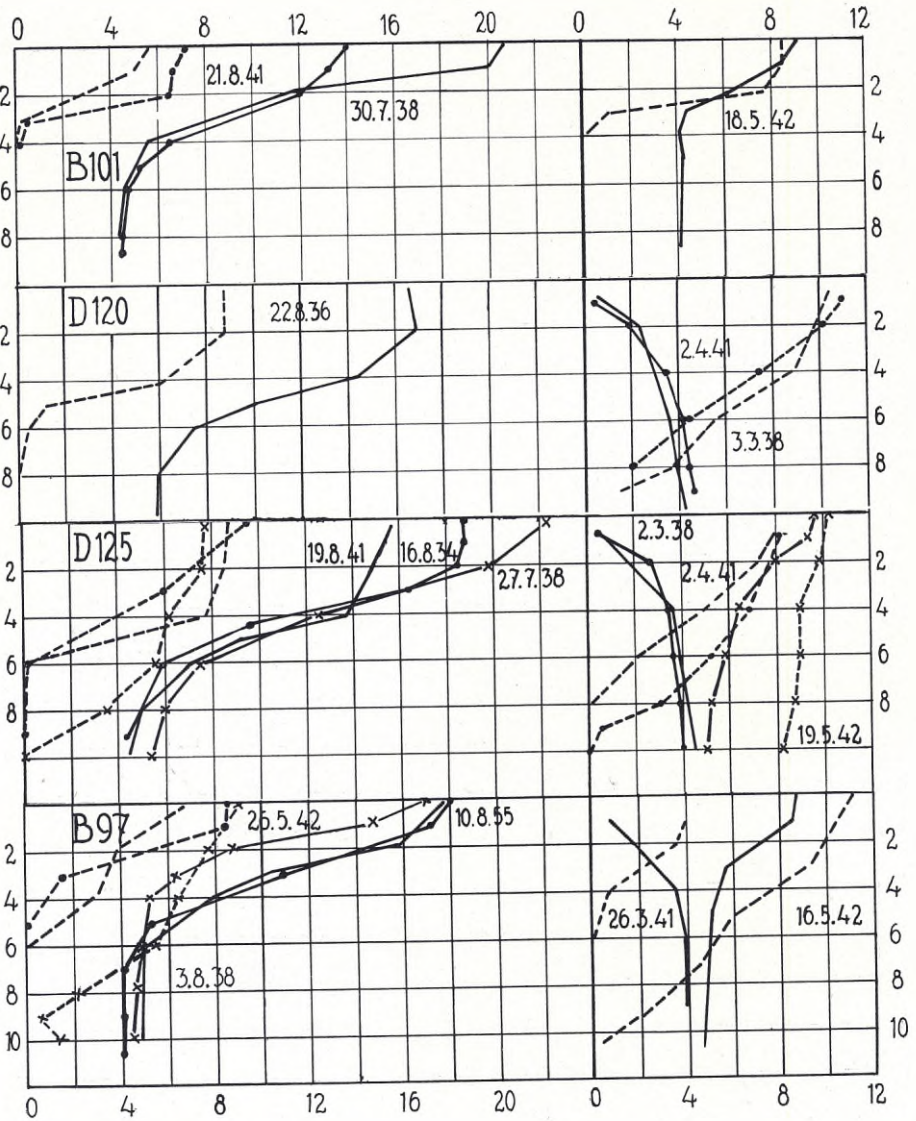


Fig. 7. Dasselbe wie in Fig. 5, aber Seen 8 m. tief und mehr.

B 101 Svarttjärn B.; D 120 Svarttjärn B.H.P.Q.A.E.; D 125 Abborrtjärn 2, B.H.; B 97 Abborrtjärn, B.

Tabelle 4. Erfolgreiche Aussätze von Bachforellen.

See	Jahr, Alter Zahl	Gefangen und weggenommen						Gefangen und zurückgesetzt	
		Jahr	Alter	Zahl			Gew. in kg		Länge in cm
				♂	♀	Sämtl.			
Grästjärn D 69	F 36-2-150	36	3	—	—	26	1,3	17—26	—
		37	4	16	13	29	9,0	23—36	11
		38	5	5	8	13	5,7	31—38	—
		39	6	—	—	6	3,6	33—40	—
		Sämtl.			74	19,6			
" " "	H 51-1-600	52	2	—	—	18	1,7	16—25	9
		53	3	6	—	8	2,4	22—36	—
		54	4	—	1	1	0,5	37	—
		55	5	1	—	1	0,7	40	—
		Sämtl.			28	5,3			
Ö. Vontjärn D 73	F 37-3-80	37	4	—	—	25	5,5	21—31	—
		38	5	3	3	6	3,1	31—43	—
		39	6	—	—	4	5,9	32—56	—
		Sämtl.			35	14,5			
Libergstjärn C 228	F 52-2-60	52	3	—	—	10	0,9	16—19	3
		53	4	—	—	6	0,6	18—19	2
		54	5	—	—	12	1,5	21—26	—
		55	6	—	—	1	0,2	24	—
		Sämtl.			29	3,2			
S. Kyrktjärn C 209	S 42-?-200	42	?	—	—	7	0,5	18—23	—
		45—50	?	—	—	11	3,8	25—45	—
		Sämtl.			18	4,3			
Stockbergstjärn A 106	F 36-1-150	36	3	—	—	19	5,2	21—36	—
		37	4	—	—	2	0,5	29—30	—
		Sämtl.			21	5,7			

lich zeigen Exempel von Seen, bei denen man mit Wahrscheinlichkeit immer, auch unter langen Eiswintern, mit einem gewissen O₂-Gehalt rechnen kann.

Aussätze von zweijährigen Bachforellen erfolgte fünfmal. Ein sehr gutes Resultat eines solchen zeigte der oben genannte Grästjärn. Von 150 zweijährigen Bachforellen erhielt man im Verlauf von 4 Jahren bis zu 74 Stück also 50 %. Der grösste Fisch war wie bei dem vorherigen Aussatz 40 cm gross, das gemeinsame Gewicht 19,6 kg. Fig. 8 zeigt die Grössenverteilung der bedeutenderen Fangjahre. Ein Aussatz von zweijährigen Bachforellen ergab im Libergstjärn C 228, wo früher Barsch ausgesetzt worden war, von 60 Ex. 29 Wiederfänge, in zwei anderen Seen, dem N. Kyrktjärn C 208 mit Barsch und dem Lejonrostjärn C 205 mit Coregonen (siehe S. 8) nur 10 bzw. 8 Wiederfänge mit 42 cm grösster Länge. Beide Seen haben einen verhältnismässig hohen O₂-Gehalt (Fig. 6). Die schlechten Resultate sind deshalb be-

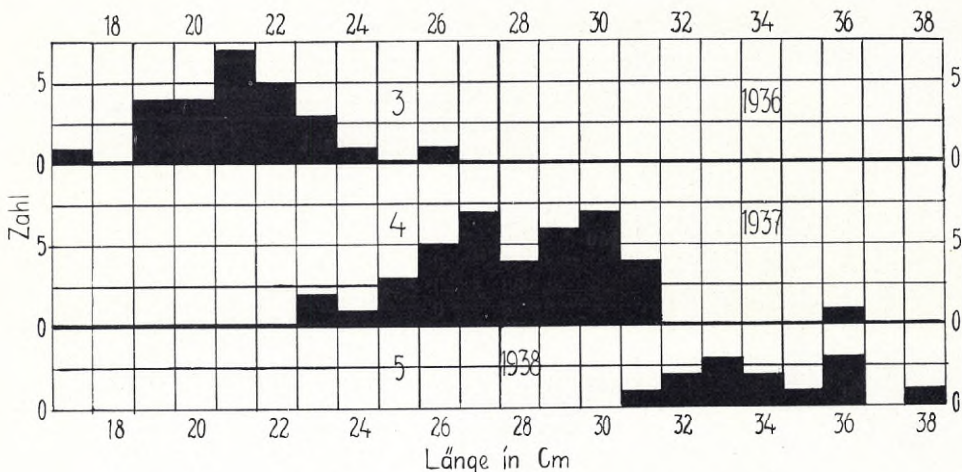


Fig. 8. Bachforelle, Grästjärn D 69.

Zahl und Grösse der wiedergefangenen Fische. Die Ziffern 3, 4, 5 geben das Alter der Fische an. Dasselbe in allen Figuren 9—27.

merkwürdig. Im Lilltjärn D 67 mit Hecht war das Ergebnis vollständig negativ.

In dem damals fischleeren Ö. Vontjärn D 73 erhielt man von 80 ausgesetzten Exemplaren dreijähriger Bachforellen 35 Wiederfänge, mit einer Länge von 56 cm und einem Gewicht von 2 kg des grössten Fisches. Im S. Kyrktjärn C 209, in dem in einem Bach gefangene ältere Bachforellen von 12—15 cm ausgesetzt worden waren, erhielt man von 200 Ex. 18 Wiederfänge mit einer grössten Länge von 45 cm. In einem weiteren See dem V. Holmtjärn, A 146, in dem dreijährige Ex. ausgesetzt worden waren, wurden keine Wiederfänge erhalten, vermutlich auf Grund von Barsch-Vorkommen oder O₂-Mangel. (Der See ist nicht untersucht.)

Seeforelle (*Salmo trutta lacustris* L)

Von der Seeforelle wurden 8 Aussätze von Brut und 8 solche von einjährigen Exemplaren gemacht. Nur in einem Fall, in dem fischleeren Hundtjärn D 70, in den 1000 Brut ausgesetzt worden waren, (Tab. 5 und Fig. 9) erhielt man ein gutes Resultat. In einigen Fällen war das Resultat mittelgut, im Grästjärn D 69 betrug doch die grösste Länge 46 cm. Die übrigen Aussätze von Brut und einjährigen Exemplaren waren negativ. In der Mehrzahl der Seen gab es von Anfang an Barsch und Hecht, in anderen Seen beruhten die Fehlschläge wahrscheinlich auf O₂-Mangel während des Winters, so z.B. im Bytjärn B 98 (im Winter nicht untersucht) und vielleicht im Barntjärn B 118 (Fig. 4). Im Hundtjärn mit seinen guten Resultaten war der O₂-Gehalt bedeutend höher (Fig. 5).

Tabelle 5. Erfolgreiche Aussätze von See- und Meerforellen, Kreuzung Bach-
× Seeforelle und Regenbogenforelle.

Fisch- art	See	Jahr, Alter Zahl	Gefangen und weggenommen						
			Jahr	Alter	Zahl			Gew. in kg	Länge in cm
					♂	♀	Sämtl.		
Seeforelle	Hundtjärn D 70	F 54-B-1.000	54	1	—	—	2		ca 10
			55	2	2	—	63	5,1	15—24
			56	3	4	—	17	2,3	22—27
			57	4	5	—	7	1,1	24—26
			58	5	—	4	6	1,9	28—37
			Sämtl.			95	10,4		
	Ö. Vontjärn D 73	F 37-3-100	37	4	—	—	19	4,4	24—30
			38	5	8	1	9	6,6	37—44
			39	6	—	—	4	5,5	48—51
			40	7	1	—	1	1,8	54
			Sämtl.			33	18,3		
			S. Kyrktjärn C 209	H 37-2-90	38	3	1	2	3
39	4	—			—	2	0,2	22	
40	5	7			6	17	4,0	25—33	
41	6	4			4	8	2,5	29—35	
Sämtl.					30	7,0			
Meerforelle	Storömyrtjärn C 160	H 36-4-48			39	7	—	—	3
			40	8	—	—	2	3,0	50—51
			41	9	5	1	6	4,8	39—47
			42	10	—	—	3	2,5	45—48
			50	18	—	—	1	1,5	58
			Sämtl.			15	13,6		
Bach- × Seeforelle	Ö. Gravtjärn C 198	H 47-1-485	48	2	—	—	11	0,7	16—19
			49	3	9	3	16	3,0	22—29
			50	4	—	—	21	10,5	26—36
			51	5	—	—	3	1,8	33—38
			56	10	—	—	2	0,4	ca 30
			57	11	—	—	1	0,2	30
			Sämtl.			54	16,6		
Regb. forelle	Ö. Vontjärn D 73	F 56-3- 3.000	56	1	3	—	12	0,1	ca 10
			57	2	3	—	7	1,5	20—27
			58	3	2	3	5	2,7	35—36
			Sämtl.			24	4,3		

Zweijährige Seeforellen wurden viermal ausgesetzt, in zwei Fällen ohne Resultat. Einer dieser Seen, Lilltjärn B 126, enthielt Barsch und Hecht, ein anderer, Abborrtjärn 1 D 126, nur Barsch, hatte aber ziemlich ungünstige O₂-Verhältnisse (Fig. 4). In den zwei anderen Seen waren die Resultate besser. Im S. Kyrktjärn C 209 mit verhältnismässig gutem O₂-Gehalt (Fig. 5), ergaben 90 ausgesetzte Exemplare 30 Wiederfänge mit einem Gewicht von 7 kg. Dieser

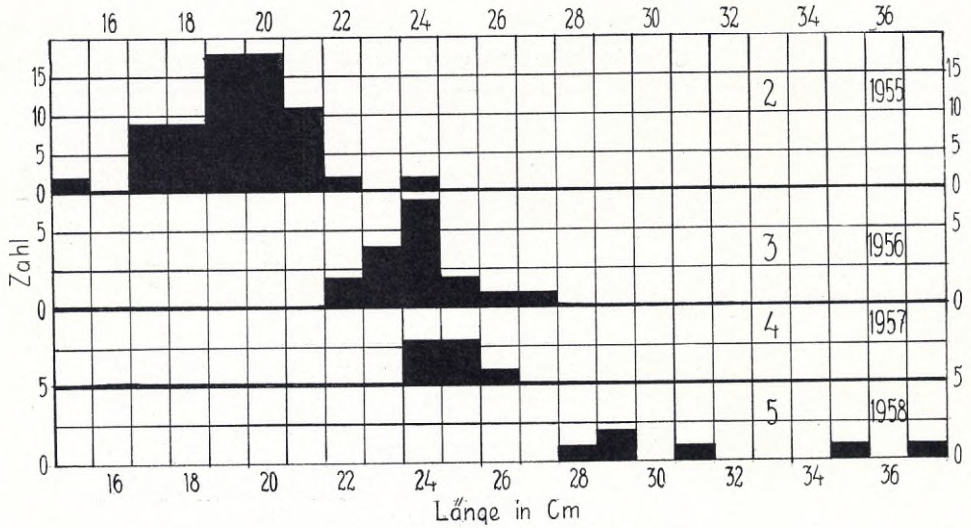


Fig. 9. Seeforelle, Hundtjärn D 70.

Aussatz fand früher statt als der oben genannte mit Bachforelle. In beiden Fällen waren die Fische in den Flossen gemerkt, wodurch dieselben leicht unterschieden werden konnten. Übrigens weisen die Wiederfänge und deren Grösse (siehe Tab. 4 u. 5) darauf hin, dass es im Jahr 1942, als die grösseren Bachforellen ausgesetzt wurden, keine Seeforellen mehr gab. Dieser See enthielt zu Anfang Barsch, doch konnte sich, wohl weil die Grösse der Barsche so klein war (ALM 1946), die ausgesetzte ziemlich grossen Forellen gut erhalten. In dem fischleeren Långsmaltjärn C 49, möglicherweise doch Elritze enthaltend, wurden von 225 zweijährigen Exemplaren 15 Wiederfänge mit 48 cm des grössten Fisches gemacht. Hier hätte man eigentlich grösseren Wiederfang erwarten können. Mit gutem Resultat wurden aber gleichzeitig Coregonen (siehe S. 46) ausgesetzt, weshalb vermutlich auch hier Nahrungskonkurrenz mit hereingespielt hat.

Ein Aussatz von dreijährigen Seeforellen im Ö. Vontjärn ergab von 100 Ex. 33 solche mit 54 cm Länge und einem Gewicht von 1,8 kg des grössten Fisches. Dieser Aussatz geschah gleichzeitig mit den schon genannten Aussätzen von Bachforelle. Die Fische wurden durch verschiedene Flossenschnitte unterschieden.

In den Seen Bodtjärn D 68 und Aborrtjärn D 77, beide mit Barsch, der letztere ausserdem mit Hecht, blieben sogar Aussätze mit dreijährigen Ex. ohne Resultat. In dem ursprünglich fischleeren Bodtjärn war der ausgesetzte Barsch (vergl. S. 52) sehr gross gewachsen und deshalb geradezu gefährlich für die Forellen, trotz deren Grösse. Die Anzahl ausgesetzter Ex., im Bodtjärn mit 44 Stück und im Aborrtjärn mit 13 Stück, war ja auch sehr klein. Ein

Aussatz von 21 Ex. vierjähriger Seeforellen in dem verhältnismässig grossen Harsjön D 128, mit einem reichen Bestand an Barsch und Hecht, war ebenfalls ohne Resultat.

Meerforelle (*Salmo trutta trutta* L)

Versuche mit dieser Forellenform haben durchgehend spärliche Resultate gegeben, was Brut und ein- bis zweijährige Jungen betrifft. Die Ursache scheint die gleiche zu sein wie bei den vorigen Forellenformen, das heisst das Vorkommen von Barsch, in mehreren Seen auch von Hecht und in einem See, dem schon genannten Lugsnjötjärn der O₂-Mangel. Nur ein einziger Aussatz hat eine grössere Anzahl Wiederfänge ergeben, nämlich im Storömyrtjärn C 160. In diesem wurden 48 vierjährige 24—37 cm lange Meerforellen ausgesetzt, von denen 15 Wiederfänge gemacht wurden, mit einem Gesamtgewicht von 14 kg. Dieser Aussatz wurde deshalb zur Gruppe 2 gerechnet. In diesen See gab es auch Barsch und Saibling. Es ist aber anzunehmen, dass die Tiefe des Sees von 17 m, sein hoher O₂-Gehalt während des Sommers auch in tieferen Regionen (Fig. 5) sowie sein vermutlich hoher O₂-Gehalt während des Winters gewisse Möglichkeiten erboten hat. Interessant ist, dass in diesem See eine Meerforelle gefangen wurde sogar 14 Jahre nach dem Aussatz. Diese war doch in schlechter Konstitution, mit einem Gewicht von nur 1,5 kg bei 58 cm Länge (Tab. 5). Zu den im übrigen schlechten Resultate hat sicher auch der Auswanderungstrieb beigetragen. Besonders in den kleinen Seen, die hier in Frage kommen, muss dieser Faktor grosse Bedeutung haben.

Forellen-Kreuzungen

Drei Aussätze von Kreuzungen verschiedener Forellen-Formen haben in zwei Seen nur eine kleine Anzahl Wiederfänge ergeben. In dem grossen Sicksjö, wurden aber sicher weit mehr gefangen als die Fangversuche ergaben. Dasselbe gilt auch für den ursprünglich fischleeren Nissetjärn, in dem sehr intensiver Raubfang getrieben wurde. Dieser Sickersee, mit zum Teil steinigem Ufern, grüner Seefarbe, Transparenz 4,9, pH 6,9 und hohem O₂-Gehalt (Fig. 6), in dem 600 Brut ausgesetzt waren, aber nur 4 Ex. wiedergefangen wurden, hat nämlich gute Resultate ergeben von mehreren anderen Aussätzen, die noch genannt werden sollen. Im dritten See, dem Ö. Gravtjärn C 198, ursprünglich fischleer, war das Resultat von Aussätzen 485 einjähriger Kreuzungen, was die Anzahl der Wiederfänge betrifft, sehr gut (Tab. 5), die Wachstum dagegen war nicht besonders gross (Fig. 10). Der See ist ein Endsee mit gelbbrauner Seefarbe, Transparenz 2,8 m und dem pH-Wert von 6,2. Die O₂-Verhältnisse sind gut (Fig. 6). Die geringe Grösse von 2,5 ha und seine Tiefe von 7 m macht, dass die Litoralzone ziemlich wenig ausgebreitet ist, und somit möglicherweise die Nahrungsproduktion nicht so gross ist. Der

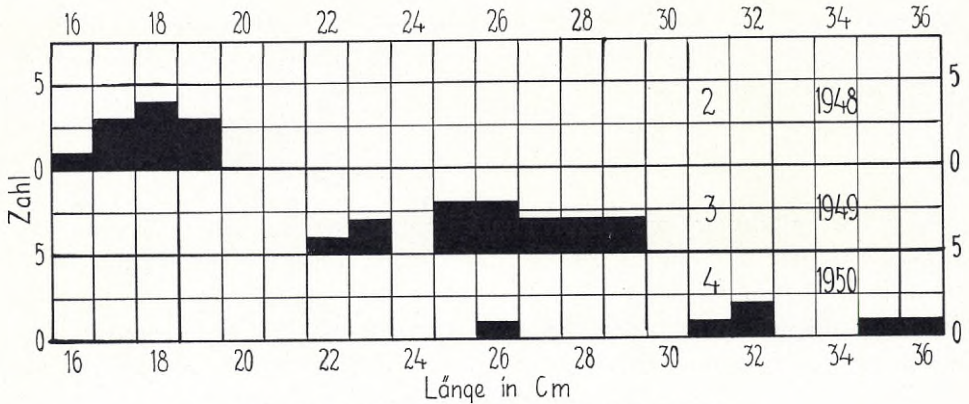


Fig. 10. Bach-×Seeforelle, Ö. Gravtjärn C 198.

schlechte Zuwachs kann also dadurch erklärt werden. (Vergl. auch einen Coregonenaussatz im selben See mit ebenfalls schlechter Wachstumszunahme (s. 47).

Regenbogenforelle (*Salmo irideus*, GIBBONS)

Diese Art ist fünfmal ausgesetzt worden, drei davon ohne Resultat. In zwei Fällen beruhte dies sicher auf dem Vorkommen von Barsch, im Harsjön D 128 auch Hecht, im dritten See dem Klingertjärn D 116, urspr. fischleer auf O₂-Mangel (Fig. 3). Die zwei übrigen Aussätze wurden im Ö. Vontjärn, beide Male mit Brut ausgeführt. Der erste Aussatz vom Frühjahr 1942 ergab nur einen einzigen Wiederfang, was wahrscheinlich auf Konkurrenz mit früher ausgesetzten Forellen beruht. Zur Zeit des andern Aussatzes war der See doch nahezu fischleer. Keine Forellen und möglicherweise nur vereinzelte Coregonen waren zurückgeblieben. Der Wiederfang ergab 24 Exemplare mit einem dreijährigen grössten Fisch von 36 cm (Tab. 5).

Saibling (*Salvelinus salvelinus* L)

In 8 Seen wurde Saibling ausgesetzt, in zwei davon Brut und in sechs einjährige Exemplare. Einer der Brutaussätze wurde im L. Meckflotjärn B 120 mit Barsch und einem sehr niederen O₂-Gehalt während des Winters gemacht, der andere in dem ziemlich grossen Ulfsjö C 149, in dem keine direkten Fischversuche gemacht wurden. Das gleiche gilt für den See St. Öfsjön A 141, in dem doch einige Saiblinge von den dortigen Bewohner gefangen wurden. Zwei Aussätze haben indessen (wie Tab. 6 zeigt) sehr gute Resultate ergeben. Im Grästjärn, der sich wie schon hervorgehoben, für den Aussatz von mehreren Fischarten geeignet zeigte, wurden von 740 Aussätzen 126 Exemplare mit 52 cm des grössten Fisches wiedergefangen. In dem fischleeren V. Rörtjärn

Tabelle 6. Erfolgreiche Aussätze von Saibling und Bachsaibling.

Fischart	See	Jahr, Alter Zahl	Gefangen und weggenommen					Gew. in kg	Länge in cm	Gefangen und zurück- gesetzt	Bemerkungen		
			Jahr	Alter	Zahl								
					♂	♀	Sämtl.						
Saibling	Grästjärn D 69	H 40-1-740	41	2	—	—	55	4,0	16—23	—	Keine reif Einige reif Meistens reif		
			42	3	—	—	17	2,1	22—26	15			
43	4	2	12	24	5,3	25—31	9						
44	5	—	—	12	4,7	33—38	3						
45	6	6	1	7	5,2	38—42	—						
46	7	2	—	2	2,2	44—47	—						
47	8	2	—	2	2,9	44—52	—						
49	10	6	1	7	5,2	38—42	—						
Sämtl.			126	31,6									
Saibling	V. Rörtjärn C 157	H 40-1-560	41	2	—	—	6	0,6	20—25	—			
			42	3	28	3	32	6,6	27—34	20			
			43	4	6	9	15	6,8	31—36	3			
			44	5	—	—	4	2,0	33—38	—			
			45	6	—	—	8	1,5	31—36	23			
			46	7	—	—	6	3,4	33—42	8			
			47	8	15	11	26	16,4	33—44	—			
			48	9	2	2	4	2,8	39—40	—			
			49	10	5	8	13	10,4	40—46	5			
			50	11	1	—	1	1,1	44	—			
			51	12	4	4	8	9,8	42—46	—			
			Sämtl.			122	61,4						
Bachsaiibling	L. Holmtjärn C 162	F 39-1-50	39	2	—	—	2	—	27—28	—	Ein festes Bestand ist in dem Abflussbach zustandegekommen		
			44	7	—	—	30	10,0	30—35	—			
			45	?	—	—	5	0,8	20—29	—			
			48	?	—	—	36	8,2	21—30	—			
			53	?	—	—	9	3,1	25—38	—			
	Sämtl.			82	22,1								
	Ö. Vontj. D 73	H 44-1-300	45	2	16	10	26	4,9	22—28	—			
			46	3	—	—	17	10,5	30—38	—			
			Sämtl.			43	15,4						
	Abborrtjärn 3 D 123	F 33-3-50	52	?	—	—	2	—	17—18	—	In Abborrtjärn 3 D 123 ausgesetzt, davon aber in den Abflussbach her- untergewandert und in dem Abborrtjärn 1, D 125 aufgegangen. Ein festes Bestand im Bach.		
53			?	—	—	19	1,7	16—29	—				
54			?	—	—	1	0,2	25	—				
56			?	—	—	12	0,9	15—27	—				
57			?	—	—	12	1,0	—	—				
58			?	—	—	15	2,5	20—29	—				
59			?	—	—	1	0,2	—	—				
60			?	—	—	1	0,2	—	—				
Sämtl.			63	6,7									
Nissetjärn C 215	F 39-1-150	40	3	—	—	—	—	23—26	6				
		41	4	10	10	25	5,0	28—36	—				
		42	5	5	5	10	2,6	31—37	—				
		43	6	6	1	7	5,0	34—37	—				
		45	8	1	3	4	3,2	33—47	—				
	H 44-1-350	45	2	—	—	3	0,7	10—17	—				
		46	3	—	—	20	4,0	25—28	20				
		47	4	—	—	12	5,4	33—34	—				
		Sämtl.			81	25,9							

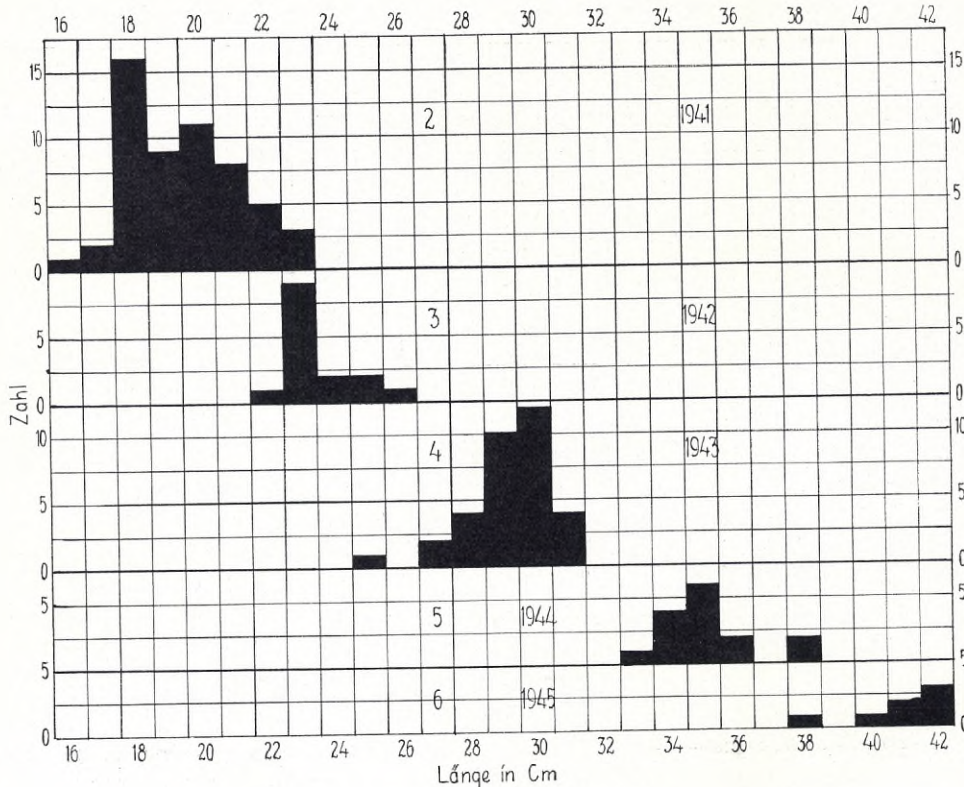


Fig. 11. Saibling, Grästjärn D 69.

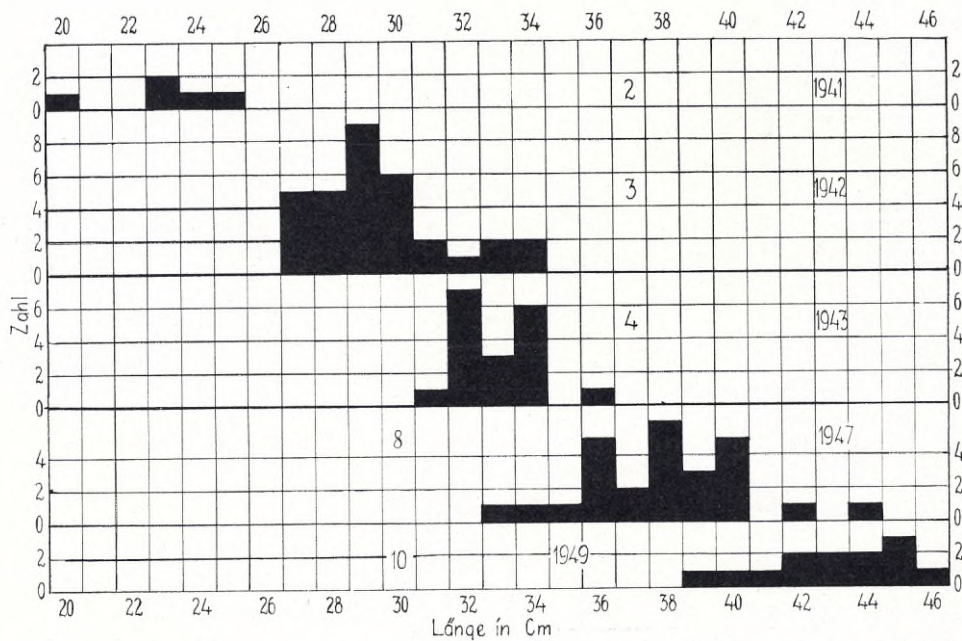


Fig. 12. Saibling, V. Rörtjärn C 157.

C 157 wurden von 560 Aussätzen 122 Exemplare erhalten. Der Saibling im Grästjärn stammte von einer kleinen Form aus Dikanäs in Lappland, der im V. Rörtjärn von einer normalgewachsenen Form des Rensjöns in Jämtland, her. Fig. 11 und 12 zeigt die Grösse bei verschiedenem Alter, der in den beiden Seen wiedergefangenen Saiblinge. Daraus geht hervor, wie auch aus Tab. 6, dass der Zuwachs durchgehend besser war im V. Rörtjärn als im Grästjärn. Dies kann sicher durch die kleinere Anzahl ausgesetzter Fische in dem nach Fläche und Volumen grösseren Rörtjärn erklärt werden. Dazu kommt, dass sich im Grästjärn früher ausgesetzte Exemplare der Coregonen und Forellen befanden, während der Rörtjärn fischleer war.

Bachsaibling (*Salmo fontinalis* L)

Nicht weniger als 14 Aussätze wurden mit Bachsaibling gemacht, davon zweimal im gleichen See. In 11 Fällen wurden einjährige Fische angewandt, die in 5 Fällen nahezu oder ganz negative Resultate ergaben. Die O₂-Verhältnisse waren im Barntjärn ungeeignet, im Långtjärn B 95 und Abborrtjärn B 97 dagegen ziemlich geeignet. Im Långtjärn wie auch im Myrbærtjärn C 165 kam Barsch vor. Im schon genannten Storörmyrtjärn, in den Meerforellen eingesetzt wurden, und die sich dort einige Jahre hielten, sind zwei Aussätze von Bachsaibling nicht gelungen, wahrscheinlich auf Grund von Konkurrenz mit Meerforelle.

In einigen Seen wurden dagegen gute Resultate erhalten. So wurden im Frühjahr 1939 von 150 Aussätzen im Nissetjärn, ohne Ablauf, 46 Exemplare und von einem späteren Aussatz im selben See im Herbst 1944, 35 Exemplare wiedergefangen. Die Grössenverteilung hat das Auseinanderhalten dieser beiden Aussätze möglich gemacht (Fig. 13). Von den ersteren haben einige Exemplare eine Länge von 45—47 cm erreicht. In diesem See, in dem wie schon oben berührt, intensiver Raubfang getrieben wurde, würden sicher die wahren Wiederfänge bedeutend höher gewesen sein.

Auch in dem für neue Arten deutlich geeigneten Ö. Vontjärn sind gute Wiederfänge erhalten worden, nämlich 43 Exemplare, alle im Verlauf von zwei Jahren gefangen. Darnach waren trotz gründlicher Fangversuche die Fische vollständig verschwunden.

Im kleinen Holmtjärn C 162 mit seinem steinigen Abflussbach, entstand ein fester Bestand, so dass dort nun Bachsaiblinge in verschiedenen Grössen gefangen werden können. Die Grössten hatten eine Länge von 35—38 cm. Der See selber hat totalen O₂-Mangel während des Winters (Fig. 3), doch wird das Wasser des Baches offenbar durch die kleinen Stromschnellen Sauerstoffbereichert und ermöglicht dadurch das Fortleben.

Zwei Aussätze von Bachsaibling betrafen drei- und vierjährige Jungen. Die letzteren, nur 40 Exemplare von 17—29 cm Länge, die im Harsjön ausgesetzt waren, konnten wie die Mehrzahl der übrigen Aussätze in diesem See nicht

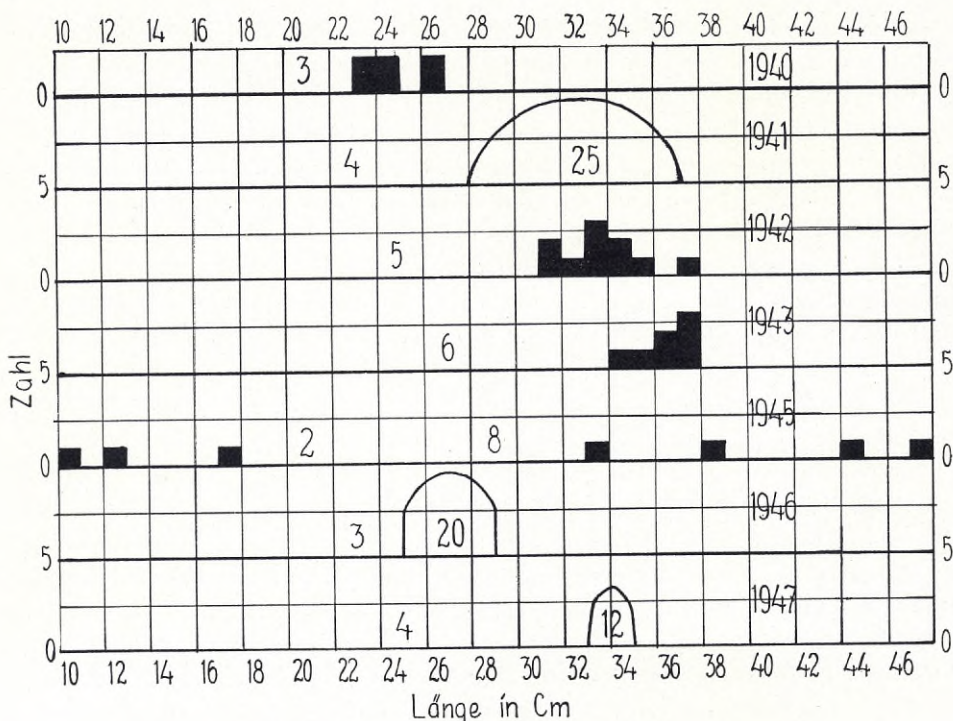


Fig. 13. *Bachsaibling*, Nissetjärn C 215.

Die Zahlen 25, 20 und 12=die Anzahl der wiedergefangenen Fische, von welchen nur der kleinste und grösste gemessen wurden.

mehr aufgefunden werden. Ein Aussatz von 50 dreijährigen 12—20 cm langen Jungen geschah im Abborrtjärn 3 D 123. In diesem See wurden indessen keine wiedergefangen. Dagegen sind die Fische den minimalen Ablaufsbach hinuntergewandert und haben dort langsam einen festen Bestand gebildet. Durch einen kleinen Seitenarm sind sie darauf weitergewandert zum Abborrtjärn 1 D 126 (vergl. Fig. 1), wo in den 1950-Jahren zusammen 63 Exemplare gefangen wurden, deren Länge zwischen 15 und 29 cm variierte. Im Abfluss des kleinen Holmtjärns wurden schliesslich von den Bewohnern bei verschiedenen Gelegenheiten von dem eben genannten Bestand *Bachsaiblinge* aufgefischt, die darauf in dem naheliegenden St. Holmtjärn C 163 ausgesetzt wurden. Doch haben sich diese offenbar nicht gegen den reichlich vorkommenden und teilweise ziemlich grossgewachsenen Barsch (Alm 1946) halten können, da nur vereinzelte Exemplare wiedergefangen wurden.

Kreuzungen *Saibling* × *Forelle* und *Saibling* × *Bachsaibling*

Vier Aussätze mit Brut wurden mit der erstgenannten Kreuzung gemacht, einer davon mit gutem Resultat. Im fischleeren L. Hälltjärn C 277 mit ver-

Tabelle 7. Erfolgreiche Aussätze von Saibling-Kreuzungen und Äsche.

Fischart	See	Jahr, Alter Zahl	Gefangen und weggenommen					Gew. in kg	Länge in cm	Gefangen und zurück- gesetzt	Bemerkungen
			Jahr	Alter	Zahl						
					♂	♀	Sämtl.				
Saibling × Forelle	La. Hälltjärn C 277	F 52-B-1.500	53	2	—	—	19	1,7	17—27	9	
			54	3	—	—	5	1,1	26—29	—	
			55	4	—	—	11	2,8	25—33	—	
			56	5	1	—	1	0,5	37	—	
			Sämtl.			36	6,1				
Saibling × Bachsaibling	Nissetjärn C 215	F 58-3-175 F 52-B-400	53	2	—	—	41	5,1	19—27	6	Möglich waren einige dieser Fische von der Kreuzung Saibl. × Forelle, die auch hier ausgesetzt wurden.
			54	3	5	4	10	5,0	28—38	—	
			55	4	—	1	1	0,3	28	—	
			56	5	—	1	1	1,4	45	—	
			58	4	—	—	14	3,5	27—32	5	
	59	5	1	3	4	2,2	33—37	—			
	Sämtl.			71	17,5						
	Svarttjärn C 279	F 52-B-5.000	53	2	20	—	55	3,0	15—20	ca 70	
			54	3	17	12	30	2,1	17—22	9	
			55	4	12	29	41	5,1	20—26	3	
56			5	4	10	14	3,2	23—31	—		
57			6	1	1	2	1,0	23—24	—		
Sämtl.			54	52	142	14,4					
St. Hälltj. C 278	F 52-B-3.000	53	2	—	—	30	2,4	19—24	ca 60		
		54	3	19	24	43	4,5	20—25	—		
		Sämtl.			73	6,9					
La. Hälltjärn C 277 B	H 55-1-20	56	2	—	—	14	0,8	14—21	10		
		57	3	—	1	1	0,4	34	—		
		58	4	—	1	1	0,6	36	—		
		59	5	1	—	1	1,0	42	—		
		Sämtl.			17	2,8					
Äsche	Ö. Von- tjärn D 73	F 49-2-170	49	3	—	—	17	3,0	22—30	7	Die meisten reif im nächsten Frühling.
			50	4	—	1	1	0,4	36	—	
			Sämtl.			18	3,4				

hältnissmässig guten O₂-Verhältnissen (Fig. 4) wurden so 36 gutgewachsene Exemplare wiedergefangen (Fig. 14), mit 37 cm des grössten Fisches. Die Resultate des Aussatzes im Nissetjärn sind unsicher, da beim ersten Probefischen Schwierigkeiten vorlagen, diese Kreuzung von gleichzeitig ausgesetzter Brut der Saibling × Bachsaibling-Kreuzung zu unterscheiden. Vermutlich war es doch die letztere die gefangen wurde (siehe Tab. 7) und nur zwei Exemplare der Saibling × Forelle-Kreuzung, die gelangen. Der Aussatz im V. Holmtjärn ist vermutlich auf Grund von O₂-Mangel missglückt (See nicht untersucht), auch der kleine und flache Lilltjärn C 321, in dem doch 7 Exemplare gefangen wurden, hat sicher sehr hohe Temperatur während des Som-

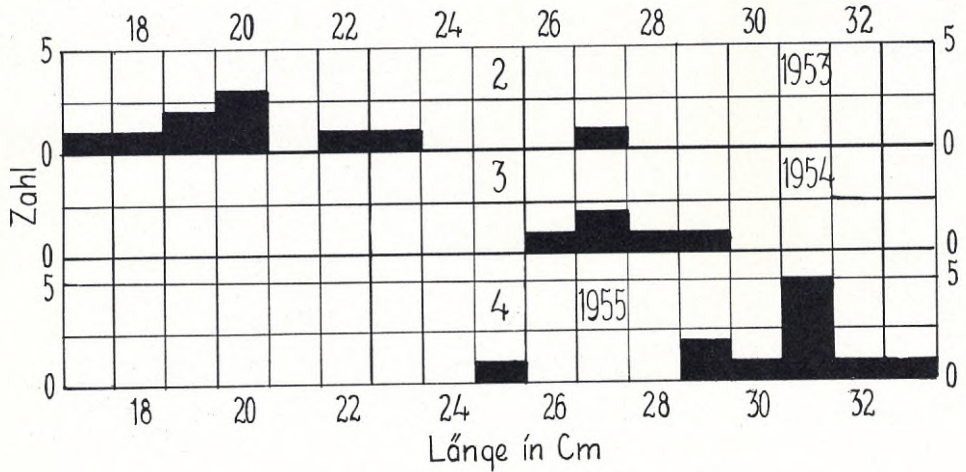


Fig. 14. Saibling×Forelle, La Hältjärn C 277.

mers und geringen O_2 -Gehalt während des Winters gehabt (Fig. 3). Wie schon in einer früheren Schrift aufgezeigt wurde (Alm 1955), muss man ausserdem bei dieser Kreuzung mit beträchtlichen Verlusten rechnen.

Bedeutend bessere Resultate wurden von der Kreuzung Saibling×Bachsaibling erhalten. Die Verluste waren bei dieser Kreuzung bei den verschiedenen Versuchen in Kälarne nicht besonders auffallend (Alm l.c.). Von den zehn Aussätzen, die Mehrzahl mit Brut, haben fünf gute Resultate gegeben, zwei waren unsicher und nur zwei waren ganz oder nahezu negativ. Letzteres betrifft die Aussätze in dem nur 0,5 ha grossen Svarttjärn B 101 mit Barsch, und in dem oben genannten Lilltjärn, in dem zwei Exemplare wiedergefangen wurden. Das beste Resultat weist der verhältnismässig grosse (8 ha), doch nur 3,5 m tiefe Svarttjärn C 279 auf, in dem im Verlauf von fünf Jahren 142 Exemplare gefangen wurden. Der Zuwachs war doch ziemlich schlecht (Fig. 15) mit einer Länge von nur 31 cm des grössten Fisches. Der See war ursprünglich fischleer, hatte gelbgrüne Seefarbe, Transparenz 3,1 m, pH 5,7 und gute O_2 -Verhältnisse (Fig. 5). Die Anzahl der ausgesetzten Brut war möglicherweise etwas zu gross, was den schlechten Zuwachs erklären kann.

Im Nissetjärn, in dem der obengenannte Aussatz der Saibling×Forelle-Kreuzung stattgefunden hat, war der Wiederfang von zwei Aussätzen der Saibling×Bachsaibling-Kreuzung hoch und der Zuwachs bedeutend besser als im Svarttjärn. Die Anzahl der ausgesetzten Brut war auch bedeutend kleiner im Nissetjärn. Weiter wurde ziemlich hoher Wiederfang mit Brut in dem fischleeren und O_2 -reichen St. Hältjärn C 278 (Fig. 5) erhalten. Da keines der wiedergefangenen Exemplare mehr als drei Jahre alt war, war das Gewicht nicht so hoch und die grösste Länge nur 25 cm. Bedeutend grössere Exemplare, bis zu 42 cm, wurden dagegen im L. Hältjärn B, C 277,

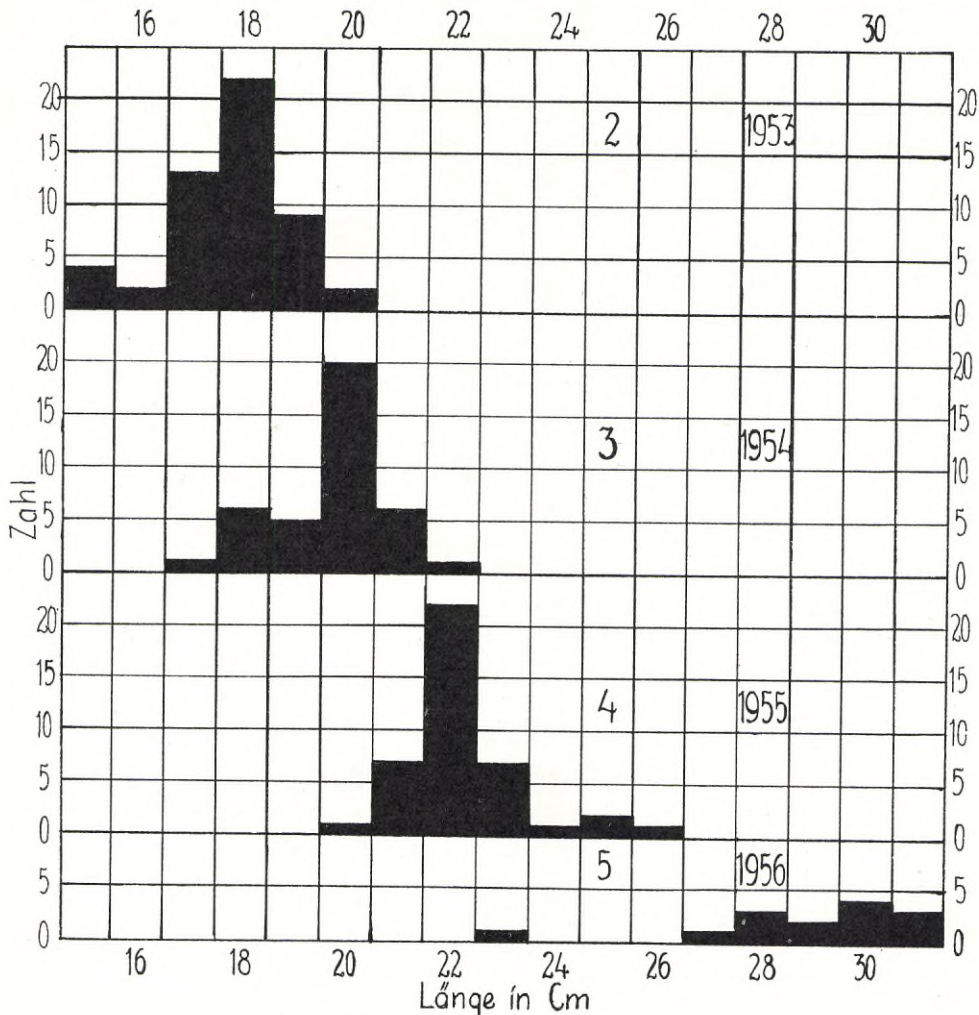


Fig. 15. Saibling \times Bachsaibling, Svartjärn C 279.

einem seichten und stark zugewachsenen, doch nicht näher untersuchten See, erhalten. Die Anzahl Wiederfänge der ausgesetzten einjährigen Exemplare betrug aber nicht mehr als 17 Stück, was sicher aus Raubfang beruht.

Äsche (*Thymallus thymallus* L)

Drei Aussätze wurden mit Äsche gemacht. In zwei Seen, beide mit Barsch und Hecht, und zwar dem Lillsjön D 67 (140 Stück zweijährige 10—18 cm lange Exemplare), und dem Hågsjön A 141 (110 dreijährige 12—20 cm lange Ex.) konnten keine Wiederfänge erreicht werden. Im dritten See dagegen, dem Ö. Vontjärn, in dem 170 zweijährige Exemplare ausgesetzt waren, wur-

den im Herbst des gleichen Jahres 17 dreijährige Äschen von 22—30 cm Länge gefangen. Im Jahr darauf wurde aber nur ein Exemplar von 36 cm und in späteren Jahren überhaupt keine erhalten (Tab. 7).

Felchen (*Coregonus*)

Verschiedene Coregonen-Formen wurden in einer grosser Anzahl von Seen ausgesetzt. Was einige dieser Aussätze betrifft, konnte nicht sicher angegeben werden, um welche Coregonenform es sich gedreht hat, auch wenn in gewissen Fällen, wie aus Tabelle 1 hervorgeht, die Fangplätze der Elternfische bekannt waren. Bei einigen Aussätzen jedoch war auch das nicht der Fall, da die Brut verschiedener Rogen durcheinander geraten war. Von solchen Aussätzen, deren Art und Herstattungsplatz nicht sicher bekannt war, zusammen 18 solche, haben 14 keine oder nur einige wenige Wiederfänge gegeben. Wie aus Tabelle 1 ersichtlich ist, drehte es sich doch meist um sehr kleine Seen, die auch Barsch, manchmal Hecht und Quappe enthielten.

Drei Aussätze wurden mit Rogen gemacht. Doch gewöhnlich wurde Brut, manchmal auch grössere Jungen verwendet, im Tormyrtjärn D 35 sogar vierjährige 20—25 cm lange solche, davon aber nur 18 Stück. Auch hier war kein Resultat zu verzeichnen, was wohl dem Faktum zugeschrieben werden darf, dass die ausgesetzten Fische von den schon vorhandenen Fischarten aufgefressen und ausgeschlagen wurden. In einigen Seen haben sich doch einzelne Exemplare gut gehalten und eine beträchtliche Grösse erreicht, so z.B. im Svarttjärn D 120 mit fünf Exemplaren und 48 cm des längsten, im Harsjön mit vier Exemplaren und 50 cm, im Bodflotjärn D 44 mit 8 Ex. und 51 cm und im Bodtjärn D 68 mit 1 Ex. von 43 cm.

Drei Aussätze mit grösseren vierjährigen Jungen, zwei davon in fischleeren Seen, haben indessen bessere Resultate gegeben, in einem Fall ein sehr gutes. Das Letztere betrifft den Grästjärn D 69, der für gewisse Aussätze wie schon angeführt sehr günstig war. Dieser Aussatz umfasste 80 Ex. von 20—27 cm Länge. Aus Tabelle 8 und Figur 16 geht hervor, dass der Zuwachs sehr gut war, wie ein neunjähriges Exemplar im Herbst 1940 zeigte mit eine Länge von 57 cm und einem Gewicht von 2,5 kg. Im Jahr 1942 erhielt man ein weiteres Exemplar von 54 cm. Während des Jahres 1941 wurde kein Ex. dieses Aussatzes gefangen, dagegen 4 Ex. mit einer Länge von 26—28 cm, die sich bei der Untersuchung als zweijährig herausstellten. In den folgenden Jahren wurden vereinzelte Exemplare desselben Jahrgangs gefangen, 1949 das älteste zehnjährige Exemplar von 51 cm. Durch die Fischereiversuchsstation hat kein neuer Coregonenaussatz stattgefunden während der Jahre 1940—41. Coregonen dieses Jahrgangs (Brut Frühjahr 1940) müssen deshalb von anderen Leuten ausgesetzt worden sein, oder aber stammen sie

Tabelle 8. Erfolgreiche Aussätze von verschiedenen Coregonen-Formen.

Fischart	See	Jahr, Alter Zahl	Gefangen und weggenommen						Bemerkungen		
			Jahr	Alter	Zahl			Gew. in kg		Länge in cm	
					♂	♀	Sämtl.				
Art und Herkunft unsicher	Grästjärn D 69	H 35-4-80	36	5	—	—	27	6,4	26—33		
			37	6	—	—	2	1,5	39—42		
			38	7	2	1	3	3,0	43—45		
			39	8	2	—	2	3,1	48—49		
			40	9	4	2	6	11,7	48—57		
			41	2	—	—	4	1,0	26—28		
			42	11	—	—	1	2,3	54		
			42	3	7	1	8	3,8	33—41		
			43	4	1	2	3	2,2	35—45		
			44	5	—	—	4	4,0	44—45		
			45	6	1	—	1	1,5	51		
			46	7	—	—	1	1,7	—		
			47	8	1	—	1	2,6	56		
			48	9	3	—	3	8,5	—		
			49	10	1	—	1	1,5	51		
			Sämtl.			67	54,8				
	Ilvästjärn D 33	H 35-4-32	36	5	—	—	19	5,0	31—37		
			37	6	—	—	3	2,7	38—42		
			40	9	—	—	1	1,4	45		
						Sämtl.			23		9,1
Långsmal- tjärn C 49	Ca 48-?-?		49	?	—	—	36	7,5	—		
			50	?	—	—	ca 60	ca 15,0	ca 30		
			51	?	1	2	3	1,4	35—36		
						ca 100			ca 24		
„Aspsik“ <i>Cor. peled</i>	Ö. Vontjärn D 73	F 45-B-25.000	45	1	—	—	10	0,6	18—20	♂ reif, ♀ nicht Sämtl. reif " "	
			46	2	—	—	75	25,7	30—35		
			47	3	—	—	33	26,4	37—43		
			48	4	—	—	22	30,0	45—51		
			49	5	4	3	8	12,9	48—54		
			50	6	—	—	4	7,6	51—55		
			51	7	1	1	2	4,2	52, 56		
			52	8	1	—	1	2,2	57		
						Sämtl.			155		109,6
			„Storsik“ <i>Cor. pidschian</i>	Ilvästjärn D 33	F 45-B-15.000	47	3	—	—		5
48	4	—				—	53	4,0	19—25		
49	5	—				—	34	1,9	19—26		
50	6	—				—	8	0,5	19—22		
51	7	3				8	31	2,4	19—28		
53	9	—				—	5	0,3	20—22		
55	11	—				—	3	0,2	22—24		
56	12	—				—	7	0,6	21—26		
58	14	11				9	20	1,2	19—24		
						Sämtl.			166	11,4	

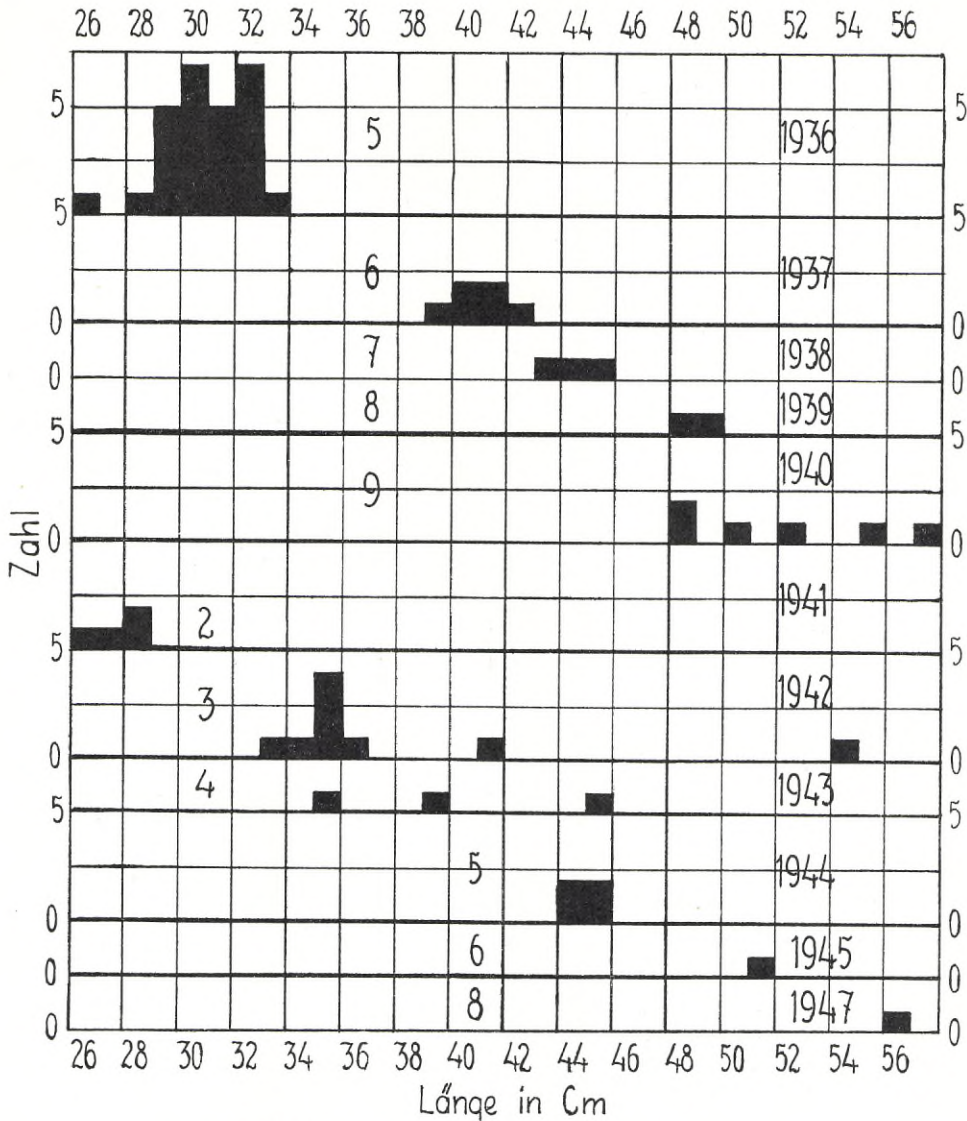
Forts.

Tabelle 8. Forts.

Fischart	See	Jahr, Alter Zahl	Gefangen und weggenommen						Bemerkungen	
			Jahr	Alter	Zahl			Gew. in kg		Länge in cm
					♂	♀	Sämtl.			
„Blåsik“, <i>Cor. lavaretus</i> × <i>Cor. oxryrhynchus</i>	Lugnsjö- tjärn D 127	F 51-B- 500	51	1	—	—	52	0,6	12—13	Vom Ansjön über- geführt, 19—27 cm, 400 ♂ und 200 ♀
			Sämtl. 40 79 119 52,9							
	Svarttjärn C 279	F 51-B-900	53	3	14	16	30	8,2	28—33	
			54	4	3	9	12	4,4	32—34	
			56	6	5	11	16	6,3	33—35	
			57	7	4	5	9	4,1	36—39	
			58	8	2	7	9	3,6	33—37	
			59	9	6	16	22	10,5	35—39	
			60	10	6	15	21	15,8	38—42	
	Sämtl. 40 79 119 52,9									
	Svarttjärn, Bräcke	F 49-B-7.500	50	2	—	—	1	0,1	25	
			51	3	13	16	29	11,1	33—37	
			53	5	—	—	31	14,1	36—41	
			54	6	7	10	17	14,4	38—45	
			55	7	—	—	8	6,2	31—46	
56			8	—	1	1	1,4	48		
Sämtl. 87 47,3										
„Smerling“, <i>Cor. lavaretus</i>	Abborrtjärn 2 D 125	F 34-?-600	34	?	13	6	19	2,8	23—28	
			35	?	8	5	13	5,5	25—32	
			36	?	6	5	11	3,1	26—39	
			38	?	—	—	1	—	—	
			41	?	3	7	10	8,0	34—49	
			42	?	5	9	14	6,5	—	
			43	?	3	3	6	4,1	32—41	
			44	?	1	2	3	2,0	—	
Sämtl. 39 37 77 32,0										

vom Laich des älteren Jahrgang des Sees. Wie Seite 69 hervorgehoben wird, wurden in vielen Seen mit guten Aussatzergebnissen Fische mit reifen Roggen und Milch gefangen, doch ohne dass irgend welche Resultate hätten bemerkt werden können. Der gelegte Roggen und die eventuell ausgeschlüpfte Brut, ist wahrscheinlich aufgefressen worden. Doch ist nicht ganz ausgeschlossen, dass in einzelnen Fällen wirklich einige Exemplare aufwachsen konnten.

Im Ilvåstjärn D 33 wurden gleichzeitig mit dem Grästjärn 32 vierjährige Exemplare ausgesetzt, auch diese 20—27 cm lang. Von diesen wurde während der folgenden 3 Jahre 23 Ex. wiedergefangen, einige über 40 cm lang. Von den Bewohnern dort wurde schliesslich etwa um das Jahr 1948 im Långsmaltjärn C 49, damals fischleer, ein Aussatz wahrscheinlich mit Brut gemacht, der etwa 100 Wiederfänge gab. Leider konnten darüber keine näheren Angaben erhalten werden.

Fig. 16. *Coregonid* (Art unsicher), Grästjärn D 69.Aspsik (*Coreg. peled* (GMELIN))

Von dieser Form, die von dem Hornavan-See in Lappland her stammt, wurde im Ö. Vontjärn im Frühjahr 1945 (SVÄRDSON 1950) Brut ausgesetzt. In dem See wahr damals sicherlich nur im Herbst 1944 ausgesetzte einjährige Bachsaiblinge vorhanden. Der Aussatz gab wie Tabelle 8 und Figur 17 zeigen, Anlass zu einem reichen und besonders schnell wachsenden Bestand, mit 155 Wiederfängen. Der Zuwachs war wie Svärdsön (l.c.) besprochen hat,

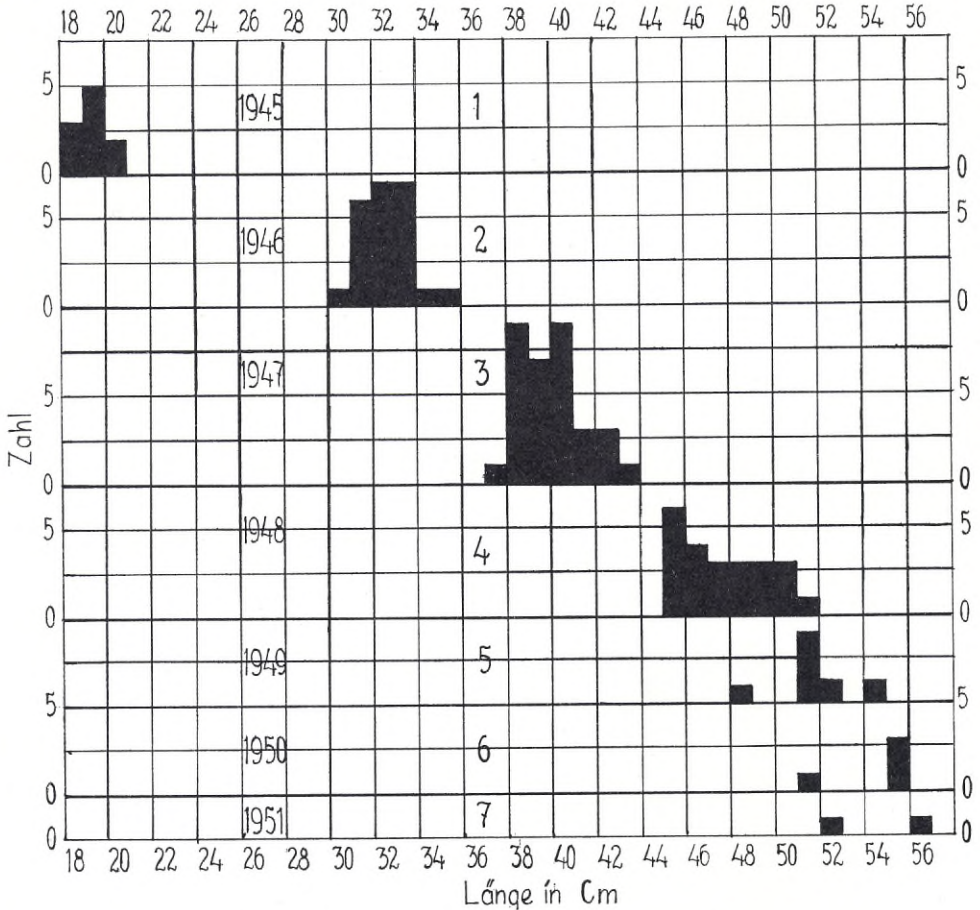


Fig. 17. „Aspsik“, *Coreg. peled*, Ö. Vontjärn D 73.

weit besser als im Ursprungssee, mit Längen von 50 cm schon bei vierjährigen Exemplaren. Als Beispiel für diesen raschen Zuwachs können von 2 Probenfängen im Jahr 1947 die Ziffern angegeben werden. Wie Tabelle 8 zeigt, wurden zusammen 33 Stück erhalten, von denen 21 Ex. am 20. August und 12 Ex. am 24. November gefangen wurden. Die Länge der erstgefangenen variierte zwischen 37 und 40 cm, die der letztgefangenen zwischen 40 und 43 cm. Die durchschnittliche Länge betrug 38,7 bzw. 41,0 cm. In späteren Jahren wurde der Wiederfang spärlicher um nach 1952 ganz aufzuhören.

Storsik (*Coreg. pidschian* (GMELIN))

Im gleichen Jahr wie im Vontjärn, wurde in dem schon genannten Ilvåstjärn D 33 ein Aussatz mit Brut des Storsik (auch von Hornavan) gemacht (SVÄRDSON l.c.). Von dem erstgenannten Aussatz in diesem See waren

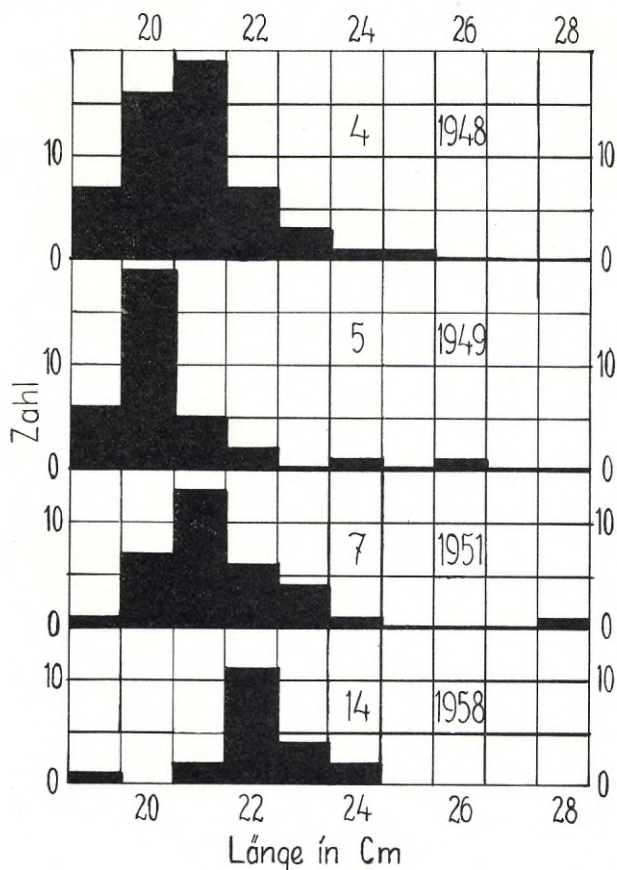


Fig. 18. „Storsik“, *Coreg. pidschian*, Ilvåstjärn D 33.

sicher keine Exemplare mehr vorhanden. Der O_2 -Gehalt des Sees ist nämlich recht nieder, wahrscheinlich herrschte während der Wintermonate der Jahre 1940—42 totaler O_2 -Mangel. Der neue Aussatz im Ilvåstjärn gab während einer langen Folge von Jahren gute Wiederfänge (Tab. 8), doch war der Zuwachs äusserst schlecht (Fig. 18). Nach einigen Jahren hörte diese ganz auf, was zur Folge hatte, dass eine grosse Anzahl der wiedergefangenen 14-jährigen Exemplare die gleiche Grösse besass wie die vierjährigen Exemplare gehabt hatten.

Blaufelchen (*Coreg. lavaretus* L. × *Coreg. oxyrinchus* L.)

Diese Coregonenform, die eine grosse Rolle im Idsjön und Gimån nicht weit von Kälärne (SVÄRDSON 1952, 1953) spielt, wurde in 20 Seen ausgesetzt, in einem davon zweimal. Alle diese Aussätze ausser einem, geschahen mit Brut. In den meisten Fällen betraf es Seen mit Barsch und Hecht. Die Seen gehörten nicht den kleinsten Grössentypen, sondern viele waren 10—40 ha gross

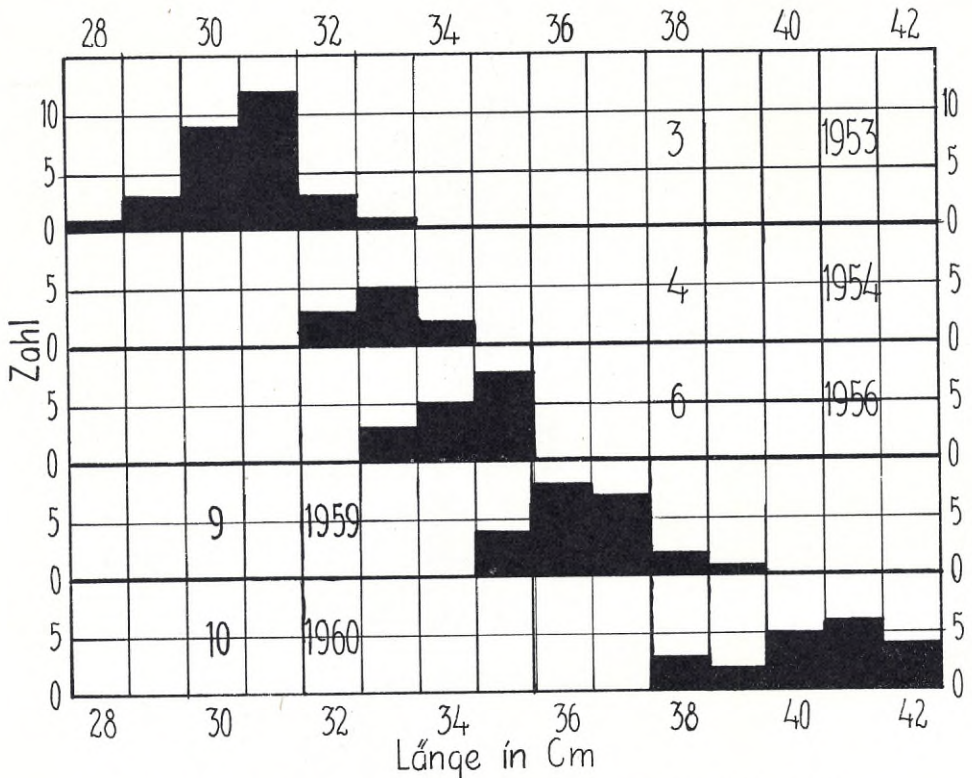


Fig. 19. „Bläsik“, *Coreg. lavaretus* × *oxyrhynchus*, Svarttjärn C 279.

und gehören wie aus der Einleitung hervorgeht zu Gruppe II und III (Tab. 1) Diese Aussätze blieben doch meist ganz ohne Erfolg. Wahrscheinlich haben Barsch und Hecht, vielleicht auch die häufig vorkommende Quappe, diese Verluste verursacht. In gewissen Seen aber, und das gilt erstaunlicherweise den kleineren, wurden einige Exemplare wiedergefangen. Dies war der Fall im S. Kyrktjärn mit 11 Ex. von 47 cm Länge des grössten Fisches, samt in den fischleeren Seen Kapelltjärn C 207 mit 6 Wiederfängen, aber nur im ersten Jahr und einer grössten Länge von höchstens 20 cm, und dem Lilltjärn C 321, wo von 7 wiedergefangenen Exemplaren auf drei Jahre verteilt ein Ex. 38 cm erreichte. Was den O₂-Gehalt dieser Seen betrifft, wurde schon oben hervorgehoben, dass dieser im S. Kyrktjärn (Fig. 5) verhältnismässig gut ist, weniger gut dagegen im Lilltjärn (Fig. 3), doch ist er offenbar hier nicht niedriger als dass wenigstens einige Exemplare auch die Winter überstehen konnten. Der nur 2 m tiefe Kapelltjärn hat wahrscheinlich totalen O₂-Mangel wenigstens in gewissen Wintern (Fig. 4).

In drei fischleeren Seen wurden indessen gute Resultate erreicht. In einem davon, dem Lugnsjötjärn, der schon als O₂-arm angeführt wurde, betrafen

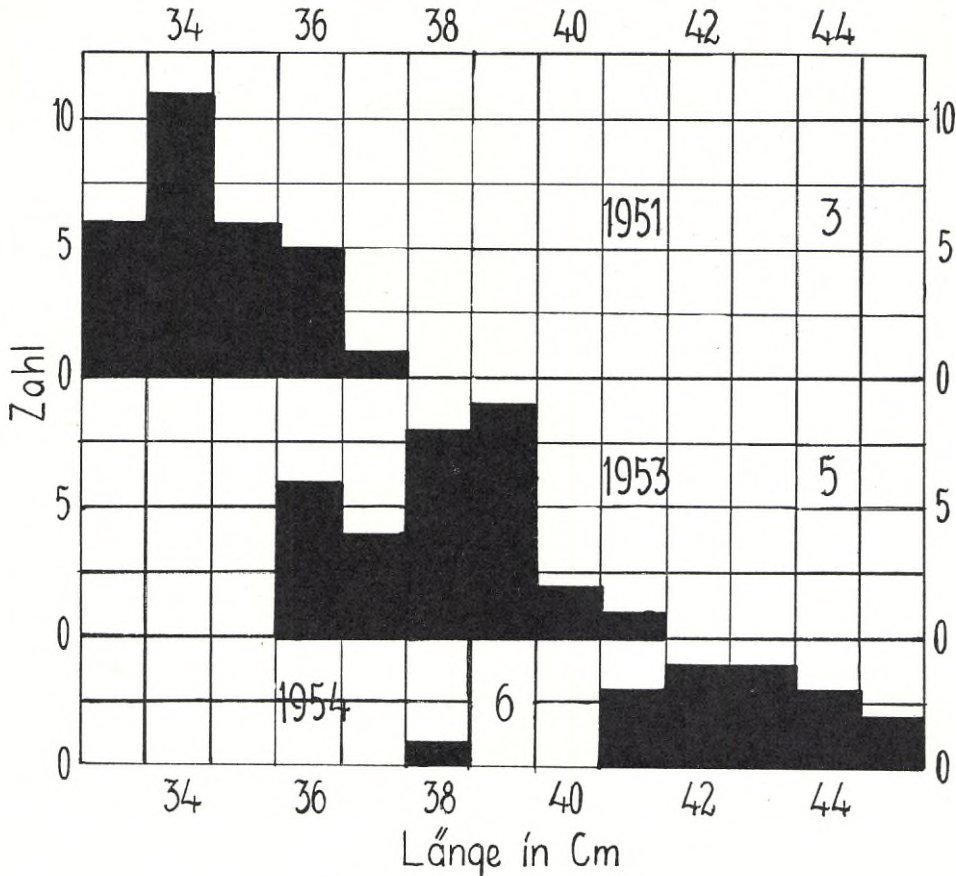


Fig. 20. „Blåsik“, Svarttjärn Bräcke.

allerdings die Wiederfänge nur den Herbst desselben Jahres, in dem die Aussätze gemacht worden waren. Im darauffolgenden Winter sind die übrigen offenbar umgekommen als Folge des totalen O_2 -Mangels. In den zwei anderen Seen, dem Svarttjärn C 279 und dem Svarttjärn Bräcke, wurden dagegen viele Jahre hindurch Wiederfänge erreicht (Tab. 8). Der Zuwachs ist in beiden Seen gut gewesen (Fig. 19 und 20), und zwar besonders im Svarttjärn Bräcke, in dem fünfjährige Exemplare über 40 cm erreichten. Im Svarttjärn C 279 wurden wie oben schon genannt auch mit Saibling-Kreuzungen ausgezeichnete Resultate erhalten.

„Smerling“ (*Coreg. lavaretus* L)

Vom Ansjön bei Kälarna, wo eine kleingewachsenen Coregonenform sehr gewöhnlich ist, wurden im Winter 1934 600 Exemplare in den Abborrtjärn 2 D 125 überführt, etwa 400 männlichen und 200 weiblichen Exemplaren mit

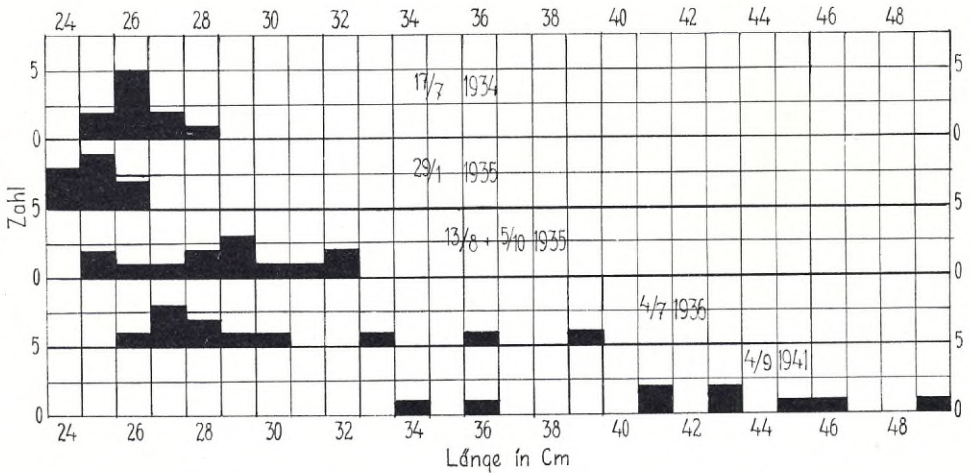


Fig. 21. „Smerling“, *Coreg. lavaretus*, Abborrtjärn 2, D 125.

einer Länge von 19—27 cm. Im Verlauf von zehn Jahren wurden 39 männliche und 37 weibliche Exemplare wiedergefangen. Dies zeigt, dass die Sterblichkeit bei den ersteren grösser war, entweder verursacht durch den Transport, so dass die Verluste bald nach dem Aussatz eintraten, oder aber erst später verursacht. Indessen müssen in diesem See von 6,5 ha die Aussätze als geglückt angesehen werden, trotz dem Vorkommen von Hecht und einem reichen Barschbestand, der in gewissen Jahren bis zu einigen tausend Exemplaren berechnet wurde (Alm 1946). Der Zuwachs geht aus Figur 21 hervor.

Brut vom Rogen dieser Coregonenform im Ansjön wurde im Allmännigtjärn C 292 ausgesetzt. In diesem 4 ha grossen See mit Barsch und Hecht, fielen die Probefänge 1, 3 und 5 Jahre nach dem Aussatz ganz negativ aus. Erst bei einem späteren Probefang nach weiteren 5 Jahren wurde ein Ex. von 43 cm erhalten. Ein Probefang 3 Jahre später gab kein Resultat.

Kreuzung Blaufelchen (*Coreg. lavaretus* × *Coreg. oxyrhynchus*) × „smerling“ (*Coreg. lavaretus* L)

Ein Aussatz dieser Kreuzung mit Brut im Ö. Vontjärn im Frühjahr 1953, zu der Zeit also, da der eben behandelte Jahrgang der Aspsik ausgegangen war, gab im Verlauf von zwei Jahren 47 Wiederfänge (Tab. 9). Der Zuwachs war sehr schlecht, besonders verglichen mit der des Aspsik. Dies kann kaum auf Übervölkerung beruhen — auf 6.000 Brut der Kreuzung kamen 25.000 des Aspsiks. Es kann jedoch die Möglichkeit bestehen, dass der reiche Bestand des grossgewachsenen Aspsik in den vorhergehenden Jahren die als Nahrung geeignete Fauna so stark dezimiert hat, dass der Nahrungszugang während einiger Jahre zurückgegangen war.

Tabelle 9. Erfolgreiche Aussätze von verschiedenen Kreuzungen mit kleinen („bläsik“, „smerling“) und grossen („storsik“) Coregonen-Formen.

See	Jahr, Alter Zahl	Gefangen und weggenommen						Bemerkungen		
		Jahr	Alter	Zahl			Gew. in kg		Länge in cm	
				♂	♀	Sämtl.				
Ö. Von- tjärn D 73	F 53-B- 6.000	53	1	—	—	24	0,6	11—17	♂ reif ♀ nicht	
		54	2	—	—	23	2,4	22—27		
		Sämtl.					47	3,0		
Grästjärn D 69	F 52-B- 2.000	52	1	—	—	36	1,0	14—16		
		53	2	43	17	174	23,6	19—28		
		54	3	36	44	80	26,1	31—36		
		55	4	1	1	2	1,1	38		
		56	5	4	2	6	3,6	39—44		
		57	6	1	—	1	0,5	39		
		58	7	1	1	2	1,6	40—41		
		Sämtl.					86	65		301
	F 55-B-7.500	55	1	—	—	50	1,0	11—14		
		56	2	16	2	78	2,3	14—17		
		57	3	21	19	40	2,2	18—21		
		58	4	37	32	69	3,5	18—23		
		59	5	22	16	38	2,1	18—24		
		60	6	23	22	45	2,5	19—23		
Sämtl.					119	91	320	13,6		
V. Rörtjärn C 157	F 55-B- 7.500	55	1	—	—	5	0,2	16—19		
		56	2	6	10	16	3,4	22—30		
		58	4	3	1	4	3,9	41—46		
		Sämtl.					25	7,5		
Abborrtjärn 1 D 126	F 55-B-2.500	56	2	—	—	15	1,2	19—23	Zum teil reif Im frühjahr gefangen	
		57	3	—	—	1	—	22		
		58	4	5	6	11	2,3	23—33		
		60	5	—	—	3	0,6	29—31		
		Sämtl.					30	4,1		
Långsmaltjärn C 49	F 55-B-7.500	56	2	3	—	32	0,7	13—15		
		57	3	—	—	13	0,3	14—16		
		58	4	35	29	64	1,4	14—17		
		59	5	8	3	11	0,5	14—23		
		60	6	18	26	44	1,5	15—25		
		Sämtl.					61	58		164

Kreuzungen „smerling“ (*Coreg. lavaretus* L.) × „storsik“
(*Coreg. pidschian* (GMELIN))

Sechs Aussätze wurden von dieser Kreuzung gemacht, vier davon in ursprünglich fischleeren Seen, in denen aber früher Aussätze von anderen Formen stattgefunden hatten. Die besten Resultate weist der Grästjärn auf (Tab. 9), in dem zwei Aussätze gemacht wurden, der erste im Jahr 1952,

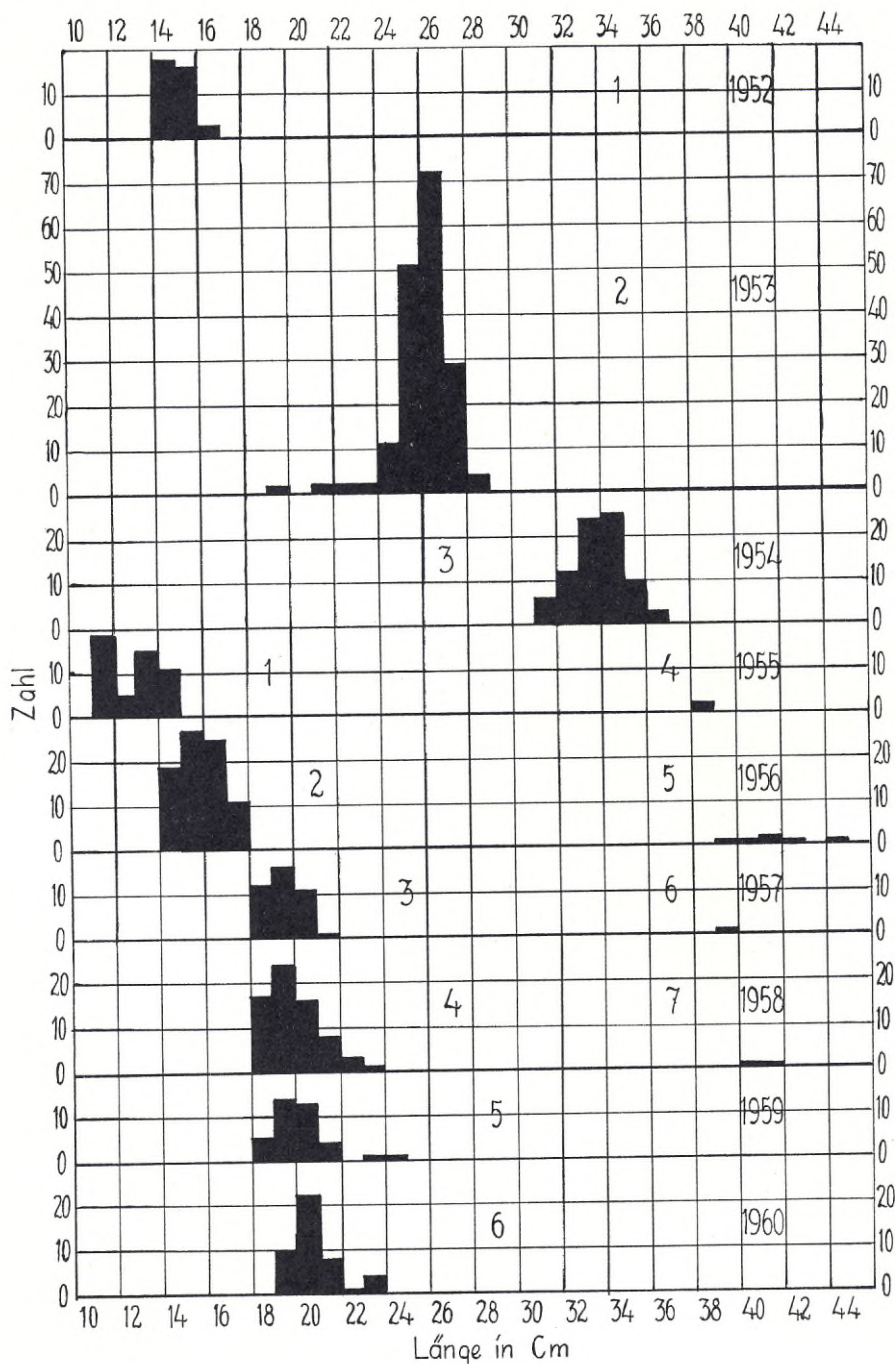


Fig. 22. „Smerling“ × „Storsik“, Grästjärn D 69.

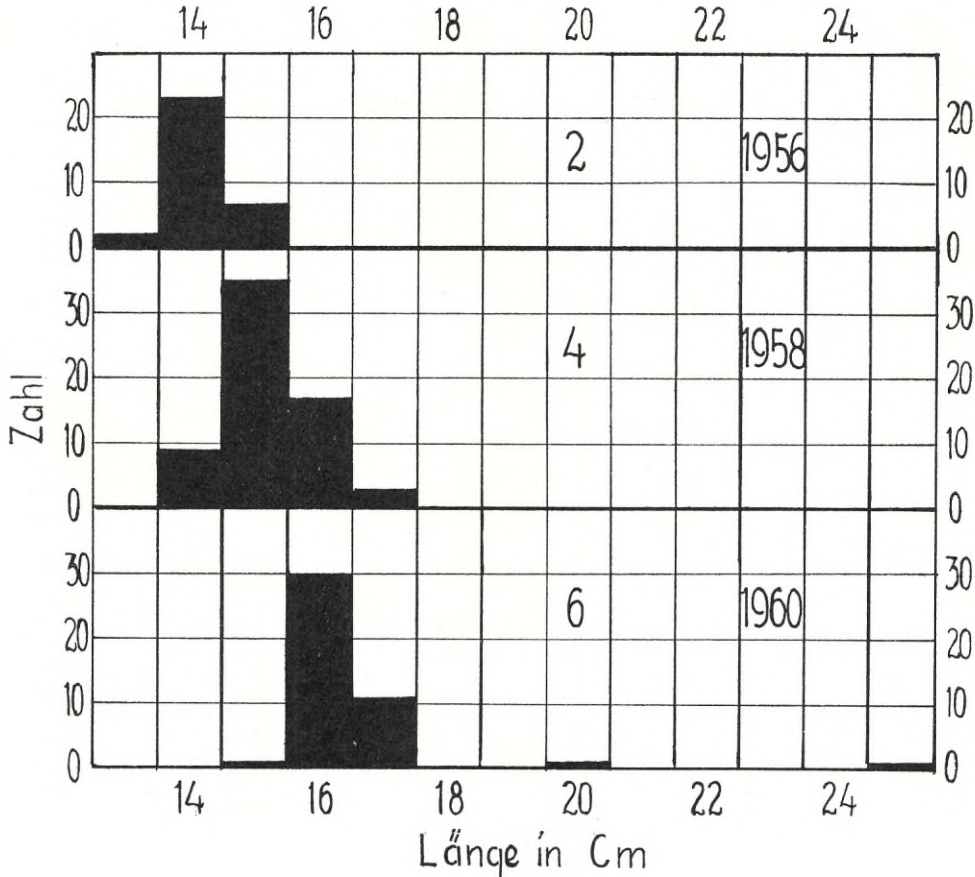


Fig. 23. „Smerling“ × „Storsik“, Långsmaltjärn C 49.

also drei Jahre nachdem das letzte Exemplar der schon behandelten Coregonenform unsicherer Herstammung gefangen worden war. Im Frühjahr 1955 erfolgte ein neuer Aussatz. Der Zuwachs war vom Aussatz 1952 verhältnismässig gut, bei den im Jahr 1955 ausgesetzten Fischen dagegen bedeutend schlechter. Es war wie Figur 22 zeigt sehr leicht diese beiden Aussätze auseinander zu halten und zu verfolgen. Die Ursache zu der auffallenden Verschiedenheit in dem Zuwachs darf teilweise der Konkurrenz mit dem schon vorhandenen Bestand des Aussatzjahres 1952, teils vermutlich dem grösseren Aussatz Brut, nämlich 7.500 im Jahr 1955 gegen nur 2.000 im Jahre 1952 zugeschrieben werden. Die Fangziffern der drei letzten Jahre weisen darauf hin, dass der Bestand des späteren Aussatzes sehr gross ist. Sicherlich kann auch im Jahre 1961 und vielleicht auch später mit weiteren Wiederfängen gerechnet werden. Von Interesse wird dabei sein zu erfahren, inwiefern einer auffallenden Zuwachs eingetroffen ist (vergl. S. 83).

Ein gutes Resultat die Anzahl Wiederfänge betreffend, zeigte der Långsmaltjärn, in dem ja der frühere Aussatz von Coregonen (siehe S. 36) ein gutes Resultat wenn auch von kurzer Dauer, gegeben hat. Was die Kreuzung betrifft, wurden in diesem See jedes Jahr zahlreiche Wiederfänge mit aber ungefähr gleich schlechten Zuwachs (vergl. S. 83) wie bei dem zur selben Zeit gemachten Aussatz im Grästjärn gemacht. Ein etwas besseren Zuwachs zeigt die Kreuzung, ausgesetzt im Frühjahr 1955 im Abborrtjärn 1 D 126, einem typischen Kleinbarschsee, 8 m tief, mit Transparenz 1,6 m und pH 6,1. Der Wiederfang indessen ergab im Verlauf von vier Jahren nur 30 Exemplare. Wahrscheinlich war die Konkurrenz mit Barsch recht gross. Allerdings waren im Winter vor der Aussetzung eine grosse Menge Barsch eingegangen, vermutlich auf Grund von O₂-Mangel (Fig. 4). Diese Dezimierung des Barschbestandes kann den geglückten Brutaussatz erklären. Die Fischversuche, die im Herbst und besonders im Frühjahr des folgenden Jahres auf Barsch ausgingen, zeigten aber, dass der Barschbestand immer noch ziemlich gross war. Der beste Zuwachs der betreffenden Kreuzung wurde von dem Aussatz im schon genannten V. Rörtjärn mit seinen guten Saiblingresultaten, erhalten. Die vierjährigen Exemplare des Jahres 1960 hatten eine Länge von 41—46 cm. Die Zahl der Wiederfänge betrug zusammen nur 25 Exemplare, die Verluste waren also offenbar gross. Der Zusammenhang des Individuenreichtums mit dem Zuwachs ist wie von Halvarsson (1959) hervorgehoben wurde, sehr auffallend in den drei eben berührten Seen.

Kleine Maräne (*Coreg. albula* L)

Der einzige Aussatz dieser Art, im Gastsjön C 66 gemacht, fiel ganz negativ aus. In dem 140 ha grossen und 9 m tiefen See (Transparenz 2,9 m, pH 6,7) kam eine Anzahl gewöhnlicher Fischarten vor, unter anderem auch eine kleinere Coregonen-Form. Es ist deshalb möglich, dass Wiederfänge von der ausgesetzten Form gemacht wurden, aber nicht von den schon vorhandenen unterschieden werden konnten.

Kreuzung Kleine Maräne (*Coreg. albula* L) × „storsik“ *Coreg. pidschian* (GMELIN))

Von dieser Kreuzung wurden acht Aussätze in verschiedenen Seen gemacht, sieben davon mit Brut. In zwei nicht näher untersuchten Seen, dem Göktjärn C 150 und dem Letjärn A 111, sind nur vereinzelte Wiederfänge gemacht, und im See Gäddtjärn A 109 wurden keine Probefänge ausgeführt. Von den übrigen Aussätzen haben drei besonders gute Resultate gegeben (Tab. 10), und zwar alle in Seen, in denen auch die Forellenaussätze ergiebig waren. Den grössten Wiederfang gewichtsmässig, doch nicht zahlenmässig, wurde im Ö. Vontjärn erhalten, in dem in den Jahren 1957—60 insgesamt nahezu 70 kg

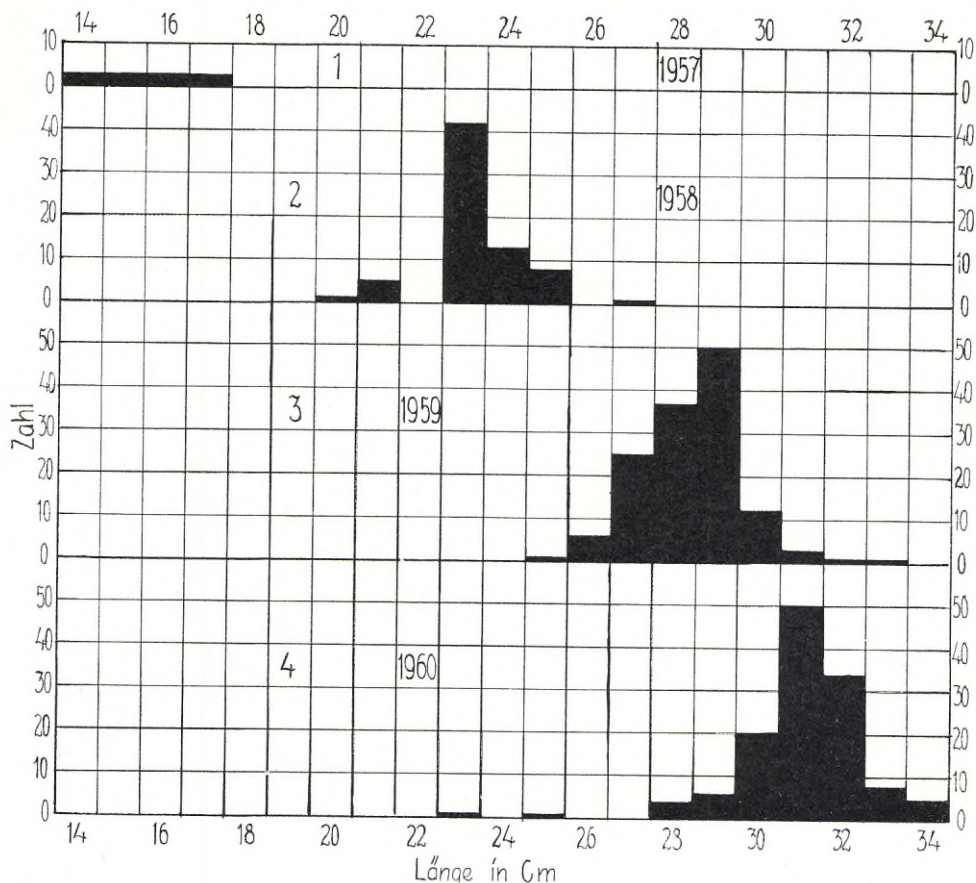


Fig. 24. Kleine Maräne \times „Storsik“, Ö. Vontjärn D 73.

gefangen wurden und sicher weitere erhalten werden können. Schon als einjährige Exemplare 14—17 cm lang, zeigten sie auch in der Fortsetzung guten Zuwachs (Fig. 24 und S. 83).

Dies gilt auch vom Hundtjärn D 70 (Fig. 25) mit einem Wiederfang von 283 Exemplare innerhalb von sieben Jahren, deren Gewicht 58,4 kg betrug. Der Aussatz im Ö. Gravtjärn ergab den grössten Wiederfang, nämlich 539 Stück auf acht Jahre verteilt. Das letzte Jahr war 1960, weshalb weitere Fänge erwartet werden können, S. 83. Der Zuwachs war indessen hier schlechter (Fig. 26), was mit Rücksicht auf den individuenreichen Bestand völlig natürlich ist. Auch das Gesamtgewicht wurde kleiner, als das der beiden vorhergehenden Seen. Ein Aussatz in einem kleinen See A 110, manchmal auch Hundtjärn genannt, nicht untersucht, gab im gleichen Herbst 27 einjährige Exemplare von 13—16 cm Länge. Die Fangversuche der folgenden Jahre waren dagegen vollständig negativ, weshalb anzunehmen ist, dass eventuell

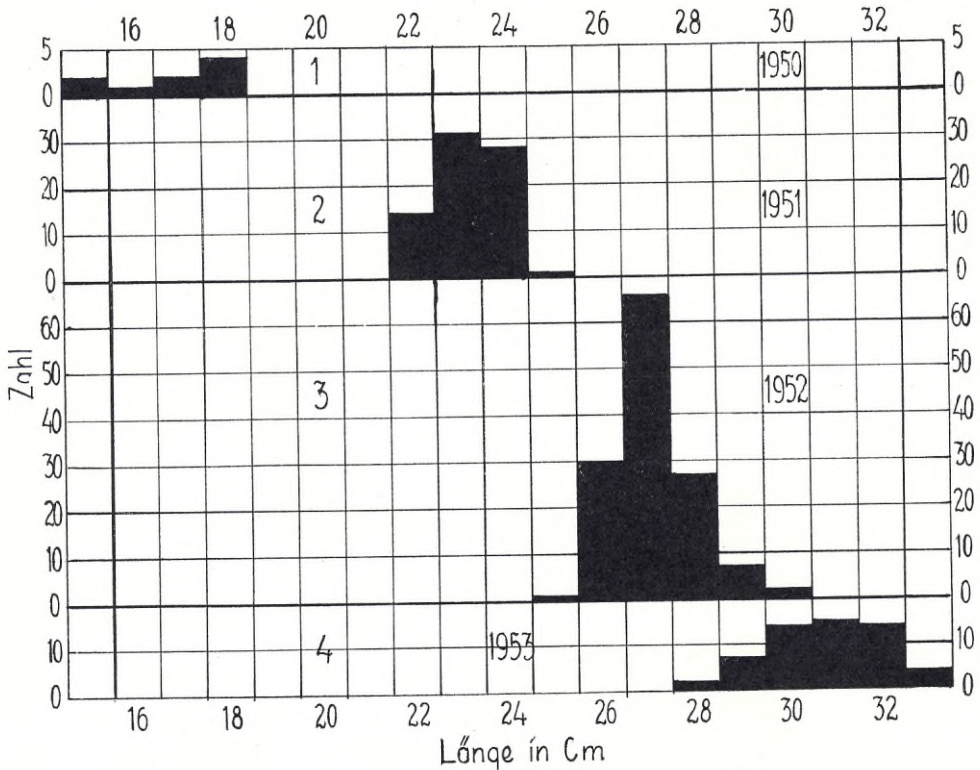


Fig. 25. Kleine Maräne × „Storsik“, Hundtjärn D 70.

übriggebliebene Exemplare aus O₂-Mangel während des Winters zu Grunde gegangen sind.

Nur ein Aussatz geschah mit einjährigen Jungen, und zwar im Dracksjön C 296, im Jahr 1957. In diesem See hatte (siehe Tab. 1) ein Brutaussatz einer Coregonen-Form, vermutlich aus dem Indalsälvs, im Frühjahr 1952 kein Resultat gegeben. Von den im Herbst 1957 ausgesetzten Kreuzung wurde im Jahr darauf nur ein zweijähriges Exemplar von 20 cm Länge gefangen. Im folgenden Jahr wurden indessen 10 Exemplare und im dritten Jahr, also 1960, ungefähr 100 Exemplare erhalten. Da letzterer Fangertag von Leuten der Gegend gemacht worden war, konnten nur ungefährliche Angaben über die Grösse der Fische erhalten werden. Die angegebene durchschnittliche Länge entspricht der im Vontjärn und Hundtjärn erhaltenen.

Zander (*Lucioperca lucioperca* L)

Im dem ziemlich grossen Hemsjön (350 ha, Tiefe 9,5 m, Transparenz 3,1 m, pH 7,0) wurden dreimal einjährige Jungen des Zander ausgesetzt. Von diesen Aussätzen sind doch keine sicheren Wiederfänge gemeldet worden, möglicher-

Tabelle 10. Erfolgreiche Aussätze von Kreuzung Kleine Maräne (*Cor. albula*)
× „storsik“, (*Cor. pidschian*).

See	Jahr, Alter Zahl	Gefangen und weggenommen						Bemerkungen	
		Jahr	Alter	Zahl			Gew. in kg		Länge in cm
				♂	♀	Sämtl.			
Hundtjärn D 70	F 50-B-7.000	50	1	—	—	9	0,3	15—18	Dazu 56, wieder aus- gesetzt
		51	2	12	61	73	8,6	22—25	
		52	3	17	116	133	29,3	25—30	
		53	4	7	40	56	13,2	28—33	
		54	5	—	3	3	1,1	23—24	
		55	6	—	6	6	3,9	36—38	
		57	8	—	3	3	2,0	36—38	
		Sämtl.		36	229	283	58,4		
Ö. Vontjärn D 73	F 57-B-8.000	57	1	—	—	12	0,4	14—17	
		58	2	21	—	70	6,6	20—27	
		59	3	48	88	136	28,1	25—33	
		60	4	81	48	129	34,4	23—34	
		Sämtl.		150	136	347	69,5		
Ö. Gravtjärn C 198	F 53-B-2.000	53	1	—	—	195	5,7	15—16	19 schon ausgelaiht
		54	2	21	10	50	4,3	20—24	
		55	3	35	37	72	7,2	20—25	
		56	4	—	—	105	11,2	22—26	
		57	5	25	29	54	6,7	22—28	
		58	6	13	13	26	3,0	20—27	
		59	7	8	9	17	2,8	25—29	
		60	8	9	11	20	3,5	26—31	
		Sämtl.		111	109	539	44,4		
Dracksjön C 296	H 57-1-2.500	58	2	1	—	1	—	20	
		59	3	2	8	10	1,5	21—27	
		60	4	—	—	ca 100	ca 20,0	ca 30	
		Sämtl.		ca 111	ca 21,5				
Tjärn A 110	F 57-B-2.500	57	1	—	—	27	0,5	13—16	

weise war die Konkurrenz von Plötzen und Coregonen gross. Wahrscheinlicher ist doch, dass der Mangel an geeigneter Nahrung von Brut und Jungen pelagisch lebender Arten die negativen Resultate verursacht hat. Der Coregonenbestand war nämlich sehr schwach und die Lieblingsnahrung des Zanders, der Stint fehlte ganz.

Barsch (*Perca fluviatilis* L)

Im Zusammenhang mit gewissen Versuchen den Zuwachs der Barsche betreffend, wurde diese Fischart in einigen fischleeren Seen ausgesetzt. In dem schon bereits genannten V. Vontjärn D 72 und dem Barntjärn B 118, wurden

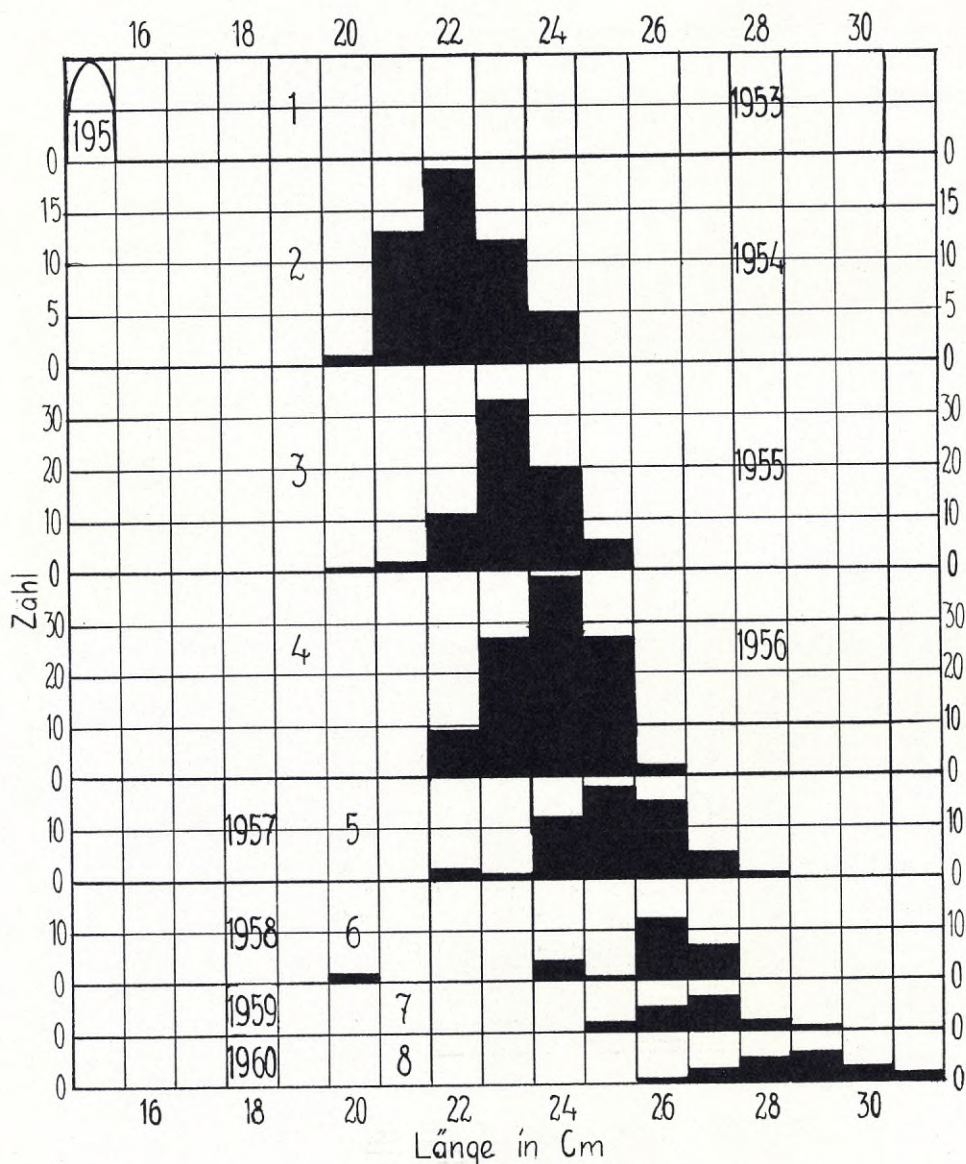


Fig. 26. Kleine Maräne × „Storsik“, Ö. Gravtjärn C 198.

vereinzelte Exemplare wiedergefangen. Von einem Brutaussatz im Vontjärn fing man im Herbst des gleichen Jahres 10 Exemplare 11—12 cm lang, dagegen keine im folgenden Jahr. Sie waren anscheinend auf Grund von O₂-Mangel eingegangen. Im Barntjärn wurde in zwei verschiedenen Jahren eine Anzahl vom Abborrtjärn 2 D 125 überführten 12—16 cm lange Barsche ausgesetzt. Die Probefänge gaben 4 resp. 5 Ex. im einen Fall mit 26—

Tabelle 11. Erfolgreiche Aussätze von Barsch.

See	Jahr, Alter Zahl	Gefangen und weggenommen						Bemerkungen	
		Jahr	Alter	Zahl			Gew. in kg		Länge in cm
				♂	♀	Sämtl.			
Bodtjärn D 68	F 36-1-300	37	3	—	—	67	5,4	16—23	1 Frühling
		38	4	16	14	30	3,6	19—26	
		39	5	8	—	13	0,6	22—27	
		40	6	—	5	5	0,8	24—29	
		42	8	—	2	2	0,5	27, 31	
		44 ¹	9	—	2	2	0,7	32, 35	
		Sämtl.					119	11,6	

28,5 cm Länge, was einen guten Zuwachs bedeutet. Auch in diesem See sind als Folge von O₂-Mangel während des Winters (siehe Fig. 4) die Fische eingegangen, die Fangversuche in den Jahren nach den Aussätzen fielen nämlich vollständig negativ aus.

Aussätze von Barsch aus dem eben genannten See herstammend, wurden ausserdem im Libertjärn C 228 und im Gröningtjärn D 115 gemacht, im letz-

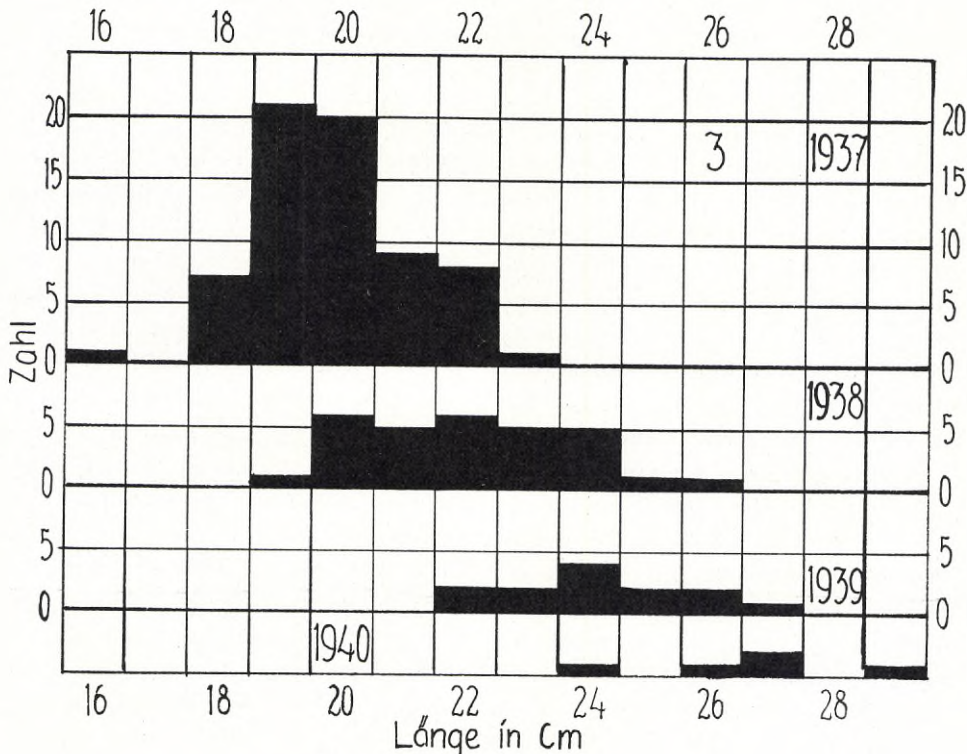


Fig. 27. Barsch, Bodtjärn D 68.

teren nur mit Weibchen. Im Libergtjärn ist ein nicht besonders zahlreicher Bestand entstanden, während im Gröningtjärn der Aussatz erfolglos blieb. Vermutlich wurden die ausgesetzten 55 Exemplare von den in diesem See früher ausgesetzten Hechten aufgefressen.

Am interessantesten ist ein Aussatz von 300 einjährigen in Teichen aufgezogenen Barsche im Bodtjärn D 68 (2,5 ha, 3,8 m tief, 2,2 m Transparenz, pH 6,0 und gute O₂-Verhältnisse). Diese zeigten einen äusserst guten Zuwachs (Tab. 11 und Fig. 27), die sich aber bei den bald auftretenden Nachkommen hastig verschlechterte. Nach ungefähr 10 Jahren war deshalb der Bestand kleingewachsen, etwa vom gleichen Typ wie der der anderen Seen der Gegend. Nähere Angaben hierüber finden sich in meinen früheren Schriften (ALM 1946, 1959).

Hecht (*Esox lucius* L)

Von der Bevölkerung wurden, nachdem was in Erfahrung gebracht werden konnte, vier Aussätze mit Hechtbrut gemacht, nämlich im Gröningtjärn D 115 etwa im Jahre 1930, im Abborrtjärn 1 D 126 ums Jahr 1932, im Stockbergtjärn A 106 ums Jahr 1950 und im Ulvsjötjärn D 103 ums Jahr 1952, in Seen also, die alle schon im Zusammenhang mit anderen Aussätzen genannt wurden. Nähere Angaben über die Resultate liegen nicht vor. Eine erhebliche Anzahl Hechte wurde doch in den beiden erstgenannten Seen gefangen.

Aal (*Anguilla anguilla* L)

In der Absicht die Resultate der Aussätze von Aal verschiedener Grösse und Herkunft zu vergleichen, wurden 8 Aussätze, die Mehrzahl in Seen mit Barsch und Hecht, gemacht. Zwei Aussätze wurden in Seen in denen früher Aal vorkam gemacht, wo aber in den letzten Jahrzehnten Aale nicht mehr beobachtet wurden. Um den auswandernden Aal fangen zu können, wurden in den kleinen Abflussbächen einfachere Aalwehre aufgeführt. Die Resultate dieser Aussätze, die sowohl mit Aalbrut vom Fluss Göta älv als von Dänemark, ausserdem mit grösseren an der Küste von Schonen gefangenen Aaljungten gemacht wurden, waren indessen in sechs der Seen ganz oder nahezu negativ. Nur in den beiden Seen in denen Aal schon früher existierte, wurden mit Angel und mit Hilfe der Aalwehre eine Anzahl Exemplare erhalten (Tab. 12). Selbstverständlich besteht die Möglichkeit, dass es hier auf natürliche Weise aufgekommene Aale gilt. Das betrifft besonders den Svarttjärn D 120, bei dem die Grösse der Aale innerhalb verschiedener Jahre stark variiert, und wo einzelne Exemplare bis zu 14 und 15 Jahren nach dem Aussatz gefangen wurden. Im Lilltjärn D 67, in dem 6 kg Aalbrut von Trollhättan (Göta älv) 1941 ausgesetzt wurde, deutet indessen die Grösse und die zunehmende Anzahl gefangener Aale darauf hin, dass sie von dem bezeichneten Aussatz herkommen.

Tabelle 12. Erfolgreiche Aussätze von Aal.

See	Jahr, Alter Zahl	Gefangen und weggenommen			
		Jahr	Zahl	Gew. in kg	Länge in cm
Svartjärn D 120	H 36-4 kg Trollhättan, Göta älv	39	4	1,8	53—82
		40	1	1,0	85
		41	2	0,9	59—72
		43	3	1,8	61—84
		44	6	3,2	56—79
		46	3	2,2	46—80
		47	2	1,6	80—81
		48	1	0,8	80
		49	3	2,0	65—81
		50	1	0,8	72
		51	4	3,2	61—84
		60	1	1,6	93
				31	20,9
Lillsjön D 67	F 41-6 kg Trollhättan	46	3	0,5	46—49
		49	9	3,6	58—69
		51	6	2,4	55—67
		54	8	4,1	58—83
		56	21	10,1	58—67
		58	1	0,8	73
		60	19	15,7	67—93
		67	37,2		

Cypriniden

Einige von den Bewohnern vorgenommenen Aussätze verschiedener Cypriniden sollen schliesslich noch genannt werden. Im Barntjärn, in dem mehrere der obengenannten Aussätze missglückt sind, auf O₂-Mangel beruhend, wurde im Jahre 1941 eine kleinere Anzahl Karauschen (*Carassius carassius* L) eingesetzt. Diese gaben Anlass zu einem sehr reichen Bestand, der offenbar weiterleben kann trotz der ungeeigneten O₂-Verhältnisse.

In dem früher genannten Libergtjärn C 228 und im Lönrostjärn C 66 wurden etwa um das Jahr 1940 Plötze (*Leuciscus leuciscus* L) ausgesetzt, die sich wenigstens im ersteren See fortgepflanzt haben und den Grund zu einem festen Bestand legten. Dies gilt auch für einen zu Anfang der dreissiger Jahre gemachten Aussatz mit der gleichen Art im Storörmyrtjärn C 160, in dem wie schon genannt von Anfang an ein fester Saiblingbestand lebte, und in dem ausserdem von den Bewohnern Barsch ausgesetzt worden war (Tab. 1 und S. 9). Auch hier entstand ein fester Bestand an Plötzen.

In dem anderen der beiden Seen, der ursprünglich Saibling enthielt, dem Ö. Rörtjärn C 158, wurden Ende der vierziger Jahre Elritze (*Phoxinus phoxinus* L) ausgesetzt. Die Absicht war, nach den Angaben der Bewohner, mehr Nahrung für den immer spärlicher auftretenden Saibling zu erhalten. Inzwischen ist aber der Saiblingbestand noch mehr zurückgegangen, sicher

auf grund von Konkurrenz mit dem rasch sich ausbreitenden Elritzbestand. Im Verlauf eines der letzten Jahre sollen während der Laichzeit im Abflussbach des Sees wenigstens 50 kg Elritze gewonnen worden sein.

IV. Diskussion über die Aussatzergebnisse

1. Vergleich der Resultate untereinander und mit Resultaten anderer Aussätze innerhalb Schwedens

In Tabelle 13 wurde von Tabelle 1 eine Zusammenfassung der Aussatzergebnisse nach dem ursprünglichen Einteilungsgrund gemacht. Wo Raubfang getrieben wurde, wären, sofern Fangziffern vorlagen, sicher verschiedene nun unter Gruppe 1 geführten Aussätze unter Gruppe 2 geführt worden. Vermutlich wären gewisse unter Gruppe 0 geführten Aussätze aus der gleichen Ursache unter die Gruppe 1 gefallen.

Die Tabelle zeigt, dass von sämtlichen Aussätzen 113 unter Gruppe 0, 30 unter Gruppe 1 und 54 unter Gruppe 2 fallen. Dies entspricht etwa 55, 14 und 26 %. Dazu kommen 10 oder ca. 5 % unsichere Fälle, die darauf beruhen, dass dort Probefänge nicht durchgeführt werden konnten.

Was die verschiedenen Fischarten betrifft, waren die Aussätze von Lachs × Forelle, Kleine Maräne und Zander ohne Resultat. Auch bei Lachs und Meerforelle waren die Resultate schlecht, während sie im übrigen sehr variierten. Die meisten 2-Resultate, verhältnismässig gesehen, zeigen Bachsaibling-Kreuzungen und Kreuzungen von verschiedenen Coregonen. Recht gute Resultate, etwa 20 %, zeigten auch Bachforelle und gewisse Coregonen.

Dass einige Fischarten bessere und andere schlechtere Resultate gegeben haben, darf indessen nicht ohne weiteres so verstanden werden, also ob die ersteren leichter in neuen Wassern einzuführen wären als die letzteren. Wie oben gezeigt und wie anschliessend mehr übersichtlich hervorgehoben werden soll, beruhen diese Verschiedenheiten in erster Linie auf den Verhältnissen in den betreffenden Aussätzseen.

Zu Anfang kann von Interesse sein, die von sämtlichen Aussätzen der Kälarne-Seen erhaltenen Ziffern mit gewissen ähnlichen früher ausgeführten Aussätzen innerhalb des Landes zu vergleichen. Zusammenstellungen solcher Aussätze wurden nämlich von den Perioden 1850—1916 vom Verfasser (ALM 1920) gemacht und von den Jahren 1917—1935 von BRUNDIN (1939). Diese Zusammenstellungen umfassen 1.401 resp. 4.113 Aussätze in 821 resp. 2.834 Seen. Leider sind die dabei angeführten Resultate nicht ganz vergleichbar mit denen der Kälarne-Seen, da die ersteren auch Aussätze in Seen umfassen, in denen die betreffenden Arten schon vorher vorhanden waren. Abgesehen von solchen Fällen war auch der Grund der Einteilung ein anderer. Die dort behandelten Aussätze beabsichtigten im Allgemeinen die Entstehung neuer Bestände. Von den ausgesetzten Fischarten wurden deshalb als geglückt solche Aussätze bezeichnet, wo dies eintraf (+ Resultat). Aussätze von

Tabelle 13. Übersicht der Resultate der Aussätze.

Fisch	Resultate				
	0	1	2	?	Sämtl.
Lachs	1	3	—	—	4
Lachs×Forelle	3	—	—	1	4
Bachforelle	20	3	6	1	30
Seeforelle	18	3	3	—	24
Meerforelle	8	1 ¹	1	1	11
Forellen-Kreuzungen	—	2	1	—	3
Regenbogenforelle	4	—	1	—	5
Saibling	4	1	2	1	8
Bachsaiibling	6	3	5	—	14
Saibling×Forelle	2	1	1	—	4
„ ×Bachsaiibl.	2	2	5	1	10
Äsche	2	—	1	—	3
Coregonen, verschiedene Arten	27	7	9	1	44
Coregonen-Kreuzungen	—	1	6	—	7
Kleine Maräne	1	—	—	—	1
Grosse×Kleine Maräne	2	—	5	1	8
Barsch	4	1	2	—	7
Zander	3	—	—	—	3
Hecht	—	2	—	2	4
Aal	5	—	2	1	8
Übrige	1	—	4	—	5
Sämtl.	113	30	54	10	207
%	54,6	14,5	26,1	4,8	

¹ Ein Aussatz mit nur 15 Wiederfängen, aber mit einem Gewicht von 13,6 kg ist zu Gr. 2 geführt.

denen gewisse Exemplare wiederfangen wurden, wo aber kein fester Stamm entstanden war, wurden als wenig geglückt (1-Resultat) bezeichnet. Vollständig missglückte Aussätze ohne jeglichen Wiederfang wurden mit 0 bezeichnet. Aussätze von Fischarten in Seen, in denen diese schon vorher vorkamen, sind oft mit ? bezeichnet worden.

Die Aussätze in den Kälarne-Seen geschahen in den meisten Fällen in Seen, von denen man wie schon genannt, von Anfang an der Überzeugung war, dass keine Fortpflanzung stattfinden konnte. Wofern aber solche Möglichkeiten vorlagen, wären wahrscheinlich die als geglückt bezeichneten Resultate von Kälarne unter ALMS und BRUNDINS + Resultate gefallen. Es müsste also möglich sein, die Ziffern der früheren + und 1-Resultate mit denen der 2- und 1-Resultate der Kälarne-Seen vergleichen zu können, trotzdem Art und Weise der Einteilung nicht ganz zufriedenstellend ist. Diese Ziffern also sind für die drei Perioden in % ausgedrückt folgende:

	Für ganz Schweden		Kälarne
	1850—1916	1917—1935	1930—1958
+ oder 2-Resultat	12,4 %	13,6 % ¹	26 %
1-Resultat	14,4 %	15,8 % ¹	14 %

¹ Diese Ziffern sind von BRUNDIN korrigiert, um sie mit den Ziffern von ALM vergleichen zu können.

Möglicherweise scheint die Anzahl der geglückten Resultate von Kälärne hoch im Vergleich mit den früheren vergleichbaren Resultaten. Auch wenn dies der Fall ist, zeigt doch der Gesamtwert für geglückte und mittelgute Aussätze, dass dieser bedeutend höher ist für die Kälärne-Seen als für die früheren Aussätze. Was diese früheren Aussätze betrifft, zeigen dagegen beide Perioden ziemlich gleichartige Resultate. Die Ursache zu den besseren Resultaten in Kälärne ist in erster Linie sicher die Tatsache, dass es sich hier um ursprünglich fischleere Seen gehandelt hat, was bei den früheren Aussätzen äusserst selten der Fall war. Auf der anderen Seite missglückte eine grosse Anzahl Aussätze in diesen fischleeren Seen auf Grund von O_2 -Mangel, ein Faktor mit dem man kaum zu rechnen hatte bei den früheren Aussätzen in schon fischführenden Seen. Ein Umstand, der möglicherweise noch dazu beigetragen hat, dass die Kälärne-Aussätze bessere Resultate gaben, wahr wohl, dass die ausgeführten Probefänge eine ziemlich zuverlässige Kontrolle über die Resultate ermöglichten, was die früheren Aussätze betreffend nicht möglich war.

2. Aussätze mit 0- und 1-Resultaten

a. Die Sauerstoffverhältnisse

Schon in der im Jahre 1960 publizierten Zusammenstellung der Resultate der limnologischen Untersuchungen in den Kälärne-Seen, habe ich im Zusammenhang mit einer Übersicht über von Anfang dort vorkommender Fischarten die Ursache zu den fischleeren Seen behandelt. In erster Linie beruht diese Tatsache auf O_2 -Mangel oder sehr niederem O_2 -Gehalt besonders während des Winters. Bei vielen Seen trifft dies jedes Jahr ein, bei anderen Seen wieder nur in gewissen Jahren mit besonderer Kälte und anhaltendem Eis, so dass die Erneuerung des O_2 -Gehaltes erschwert wurde. Was diese letzteren Seen betrifft, in denen vielleicht während einer langen Folge von Jahren feste Fisch-Bestände existiert haben, kann ein einziger harter Winter mit nachfolgendem O_2 -Mangel diese zerstören. Wo in einem solchen Fall die natürlichen Rekrutierungswege schlecht waren, (steiler Fall der Abflussbäche und Seen ohne Abfluss) konnte es natürlich lange dauern, bis der See wieder bevölkert wurde. Daran soll besonders erinnert werden. Die Abwesenheit von Fisch in einem bestimmten See braucht deshalb noch kein Beweis dafür zu sein, dass ein Aussatz nicht gute Resultate geben könnte durch eine Folge von Jahren hindurch.

Gewisse schon in den dreissiger Jahren mit gutem Resultat gemachten Aussätze von Forellen-Formen in einigen Seen mit ziemlich niederem O_2 -Gehalt während des Winters (Ö. Vontjärn und Grästjärn) zeigten, dass offenbar auch Lachsfische eine kräftige Verminderung des O_2 -Gehalts vertragen können, und dass man deshalb keine so grosse Rücksicht auf diesen Faktor zu nehmen braucht wie man anfangs glaubte.

Aus den eben berührten Gründen wurde eine grosse Anzahl Aussätze in Seen gemacht, wo man allerdings nicht sicher sein konnte, dass die O_2 -Verhältnisse kein Hindernis für ein geglücktes Resultat ausmachen, wo es aber von Interesse sein sollte die Grenze für den O_2 -Gehalt zu prüfen, die von den Fischen vertragen werden kann.

Die Resultate haben gezeigt, dass die O_2 -Verhältnisse in gewissen Seen so ungeeignet waren, dass die ausgesetzten Fische starben. Dies war der Fall mit Salmoniden und Coregonen wie auch Barsch. Wahrscheinlich ist der Fisch manchmal schon während des ersten Sommers eingegangen, z.B. in Seen mit einer sehr dünnen aber stark erwärmten Epilimnion und einer nach dem Volumen grossen, kalten und O_2 -armen oder O_2 -freien Hypolimnion. Ein Beispiel hierfür ist der Skimsåstjärn D 45 (Bachforelle) und der Bytjärn B 98 (Seeforelle). Fig. 3 zeigt, dass schon in 2 m Tiefe der O_2 -Gehalt im August nur 0,6 resp. 0,3 mg/l war, und von 3 resp. 4 m Tiefe an totaler O_2 -Mangel eingetreten war. Am 8. März 1938 gab es nur noch Spuren von O_2 unmittelbar unter dem Eis im Skimsåstjärn. Im Bytjärn, der im Winter nicht untersucht wurde, war der O_2 -Gehalt am 16. Mai 1942 schon in 4 m Tiefe = 0, was darauf deutet, dass der See von meromitischem Typ ist.

In anderen Fällen wieder war der O_2 -Gehalt während des Sommers verhältnismässig hoch. Dort wurde in den Herbstprobefängen manchmal eine grössere oder kleinere Anzahl Exemplare gefangen. Im darauffolgenden Winter trat aber O_2 -Mangel ein, was zur Folge hatte, dass die Fische eingingen und somit bei den Probefängen des nächsten Jahres die Resultate vollständig negativ ausfielen. Dies was z.B. der Fall mit Forelle und Barsch im V. Vontjärn D 72, mit Coregonen im Lugnsjötjärn, Kapelltjärn und Tjärn A 110, samt in gewissen Jahren mit Seeforelle, Bachsaibling und Barsch im Barnjärn. Aussätze im Lugnsjötjärn und Tjärn A 110 sind auf Grund der Fanganzahl im ersten Herbst, 52 resp. 27, wenn auch mit einigem Zögern zur 2-Gruppe gerechnet worden. Im Lilltjärn C 321 fiel auf Grund seiner geringen Tiefe und, wie sich bei einer Untersuchung am 22. Januar zeigte, seinem stark gesunkenen O_2 -Gehalt ein Aussatz der Saibling-Kreuzung ganz negativ aus, während ein Aussatz von Coregonen (blåsik) wenigstens 7 Wiederfänge auf drei Jahre verteilt ergab. Dies könnte möglicherweise darauf hinweisen, dass Coregonen einen etwas niedrigeren O_2 -Gehalt ertragen als die Saibling-Kreuzungen. Dafür sprechen auch die Aussätze im Ilvåstjärn von Bachforelle und Saibling, beide ohne Wiederfänge, während dagegen zwei Aussätze von Coregonen ziemlich gute Resultate die Anzahl betreffend gegeben haben, wenn auch der Zuwachs schlecht war (siehe S. 39).

In mehreren Seen haben aber doch, trotz ziemlich niederem O_2 -Gehalt Salmoniden weitergelebt. So war im Stockbergstjärn A 106 mit guten Bachforellen-Resultaten — von Anfang an auch Elritze — der O_2 -Gehalt im März 1938 schon in 1 m Tiefe nur 2 mg/l, während in 3 m Tiefe totaler O_2 -Mangel herrschte (Fig. 4). Im Libergstjärn C 228 muss man wahrscheinlich mit stark

heruntergesetztem O_2 -Gehalt während des Spätwinters rechnen, da dort schon im Januar 1955 (Fig. 4) der O_2 -Gehalt gegen die tieferen Regionen hin kräftig gesunken war, und der See als Sickersee keinen O_2 -bereichernden Zulauf hat. Trotz dieser Tatsache haben die verschiedenen hier ausgesetzten Fischarten, wenn auch nicht besonders gute Resultate erreicht, so doch mehrere Jahre überlebt. Auch im Ö. Vontjärn D 73 mit vielen guten Aussatzergebnissen, war z.B. sicher der O_2 -Gehalt während des Spätwinters 1938 ziemlich nieder, nachdem er Anfang März (Fig. 4) nur 3—4 mg/l erreicht hatte. In etwas mehr als 3 m Tiefe herrschte schon totaler O_2 -Mangel. Im Grästjärn D 69, der im April 1941 nur etwa 2,8 mg/l O_2 in den obersten Wasserschichten hatte, und mit gegen die Tiefe zu schnell abnehmend bis zu vollständigen O_2 -Mangel (Fig. 5), lebten trotzdem die im Herbst 1940 ausgesetzten einjährigen Saiblinge und älteren Coregonen weiter. Im V. Rörtjärn C 157, in dem auch ein Saiblingaussatz gute Resultate gegeben hat, waren die Verhältnisse günstiger (Fig. 5). Auch in dem harten Winter 1941 waren die O_2 -Verhältnisse hier ziemlich hoch mit etwa 6 mg/l in 2 m Tiefe, mit einer gleichzeitigen Temperatur von 2° .

Wie in dem Bericht von 1960 hervorgehoben wurde, finden sich Angaben über den O_2 -Gehalt, den verschiedene Fischarten aushalten können bei einer Mehrzahl von Forschern (u.a. MOORE 1942, COOPER und WASHBURN 1949, RAWSON und RUTTAN 1952, VALLIN 1954, MARG. BROWN 1957, SCIDMOORE 1957, MOILE and CLOTHIER 1959, RAWSON 1955, 1960). Diese Angaben weichen etwas voneinander ab. Gemeinsam für alle ist doch, dass die Grenzwerte für Fischsterblichkeit durch O_2 -Mangel, wie auch die Werte für den O_2 -Gehalt, der normales Wohlbefinden möglich macht, am höchsten bei Salmoniden und Coregonen und am niedersten bei gewissen Cypriniden sind. Die detailliertesten Versuche wurden von MOORE ausgeführt. Er setzte eine Anzahl verschiedener Fischarten, doch nicht Salmoniden, in geschlossenen Reusen in verschiedener Tiefe, in zwei Versuchsseen, aus in denen gleichzeitig der O_2 -Gehalt festgestellt wurde. MOORE konnte dabei unter anderem feststellen, dass Hecht und Barsch untertauchen wenn der O_2 Gehalt bei $25\text{--}26^\circ\text{C}$ auf 3,5 mg/l sinkt, während im Winter bei $0\text{--}4^\circ\text{C}$ erst ein so niedriger O_2 -Gehalt wie der zwischen 1 und 2 mg/l den Tod dieser Arten zur Folge hat. VALLIN (l.c.) gibt für im Aquarium ausgeführte Versuche als niedersten Grenzwert 2,5 mg/l für Coregonen an, für Forelle 1,8, für Barsch 1,0 und für Karausche 0,07, und als normale Werte 5—6 mg/l für Coregonen, Saibling und Forelle, 4 für Barsch und 1 oder 2 mg/l für Karausche. MARG. BROWN (l.c.) gibt als Grenzwert für Barsch auch etwa 1 mg/l an, während SCIDMOORE (l.c.) mit 1,5 mg/l etwas höher geht. COOPER und WASHBURN aber geben für Barsch nur 0,3—0,4 und für gewisse Cypriniden nur 0,2 mg/l als niedrigst ertragbare Werte an.

Bei den Kälarne-Untersuchungen war es nicht möglich, die unteren Grenzwerte genau festzustellen, da die Untersuchungen des jeweilig aktuellen O_2 -Gehalts nur in gewissen Fällen gemacht werden konnten. Die oben disku-

tierten Resultate deuten doch darauf hin, dass einerseits die Unterschiede der Sterblichkeitswerte bei den verschiedenen Fischarten auf Grund des niederen O₂-Gehalts nicht so gross sind wie aus den Ziffern der oben genannten Forscher hervorgeht, andererseits diese Werte in jedem Fall bei Wintertemperatur überhaupt niedriger liegen. Die oben angeführten Beispiele zeigen, dass Salmoniden und Coregonen im Winter bei einem so niederen O₂-Gehalt von nur etwa 2 mg/l, möglicherweise noch niedriger gut fortleben können. Überhaupt sind, mit Rücksicht nur auf O₂-Mangel, die Aussatzresultate nur in solchen Seen ausgeblieben, wo dieser im Sommer in schon geringer Tiefe bis zu den O-Werten heruntersank, oder wo dieser im Winter unter 1 mg/l gesunken war. Dies macht, dass man wahrscheinlich eine sehr grosse Anzahl von fischleeren Kleinseen für Aussätze verschiedener Fischarten in Anspruch nehmen kann, und dass man dabei nicht so vorsichtig zu sein braucht wie RAWSON und RUTTAN ansehen. Diese Forscher (l.c.) betonen nämlich, doch ohne Angaben direkter Grenzwerte des O₂-Gehalts, dass Seen kleiner als 1 Acre und mit einer Tiefe von höchst 5 m, sowie einer Eisdecke während einer Zeit von 5 Monaten, auf Grund der Gefahr des totalen O₂-Mangel im Winter, direkt ungeeignet für Fischaussätze sind.

b. Das Vorkommen von anderen Fischarten

Was die Ursache zu den negativen Resultaten im übrigen betrifft, ist sicher das Vorkommen anderer Fischarten besonders des Barsch die wichtigste. Diese Fischart hat ein grosses Reproduktionsvermögen und tritt oft in individuenreichen aber kleingewachsenen Beständen auf (ALM 1946). Sie ist sicher teils ein schwerer Konkurrent einer neueingesetzten Fischart was die Nahrung betrifft, teils auch ein gefährlicher Predator. Das Letztere gilt besonders den Brutaussätzen. Die vielen Fehlschläge bei den Brutaussätzen von Forellen und Coregonen in Seen mit Barsch bekommen dadurch ihre natürliche Erklärung. Oft sind auch Aussätze einjähriger Jungen in Barschseen missglückt. Doch gibt es einzelne Ausnahme. Ein Aussatz von Coregonen-Brut im Abborrtjärn 1 D 126 ist z. Beispiel geglückt, ausserdem ein Aussatz der Kreuzung Grosse×Kleine Maräne im Dracksjön.

Aussätze von grösseren Jungen in Barschseen haben im allgemeinen bessere Resultate ergeben. So z.B. zweijährige Bachforellen im Libergstjärn und Seeforellen im S. Kyrktjärn, vierjährige Meerforellen im Storörmyrtjärn samt überführte Bachforellen von Norrbäcken im S. Kyrktjärn und Coregonen „smerling“ vom Ansjön im Abborrtjärn 2. Im Bodtjärn D 68 mit grossgewachsenem Barsch (siehe S. 52) ist dagegen ein Aussatz von dreijährigen Seeforellen nicht geglückt. Die Anzahl ausgesetzter Exemplare betrug aber nur 44 Stück.

In mehreren Aussatzseen kam ausser Barsch auch Hecht vor, oft auch Quappe und Plötte. Hier waren die Aussätze auch von grösseren Jungen ohne

Resultat. Dies gilt für zweijährige Bachforellen im Lillsjön D 67, für dreijährige Seeforellen im Abborrtjärn D 77 (hier wurden nur 13 Ex. ausgesetzt) und für vierjährige Seeforellen im Harsjön D 128 (21 Ex.). In diesem See konnten auch vierjährige Bachsaiblinge nicht wiedergefangen werden. Das gleiche gilt von zweijährigen Äschen im eben genannten Lillsjön und von dreijährigen solchen im Hågsjön A 141 samt von vierjährigen Coregonen (allerdings nur 18 Stück) im Tormyrtjärn D 35. Natürlich hat auch die geringe Anzahl ausgesetzter Exemplare in den eben genannten Seen zu den schlechten Resultaten beigetragen. (Vergl. auch S. 6.)

Doch nicht allein das Vorkommen von Barsch und Hecht haben negative Resultate verursacht. Auch solche Fischarten, die bei Neuaussätzen in ursprünglich fischleeren Seen sich gut gehalten haben, waren in mehreren Fällen ein Hindernis für ein gutes Resultat einer einige Jahre später ausgesetzten anderen oder gleichen Fischart. So sind Aussätze einjähriger Bachforellen im Ö. Vontjärn D 73 (Herbst 44), und im Ilvåstjärn D 33 (Herbst 40) samt Brut derselben im V. Rörtjärn C 157 (Frühj. 54) wahrscheinlich missglückt auf Grund der in diesen drei Seen schon vorhandenen Beständen von resp. Bach- und Seeforellen (ausg. Frühj. 37) Coregonen (ausg. Herbst 35) und Saiblinge (ausg. Herbst 40). Einjährige Bachsaiblinge ausgesetzt im Storörmyrtjärn im Herbst 44 und 49 und einjährige Seeforellen dort ausgesetzt im Herbst 51 konnten sich ebenfalls nicht halten gegen die schon vorhandenen Bestände der Meerforelle, ausgesetzt im Frühjahr 1937. Wo verschiedene Arten etwa gleichzeitig ausgesetzt worden waren, konnten dagegen die Resultate gut ausfallen. Ein Exempel dafür bietet der Grästjärn. In diesem wurden im Herbst 1951 einsömmerige Bachforellen und im Frühjahr darauf Brut einer Coregonen-Kreuzung ausgesetzt, beide besonders aber die Coregonen-Kreuzung mit guten Wiederfängen.

Schliesslich kann als Ursache zu schlechten Resultaten der Auswanderungstrieb angeführt werden. Besonders bei Lachs und Meerforelle kann dieser Faktor eine grosse Rolle gespielt haben, da die Seen gleichzeitig so klein waren wie das meistens hier der Fall war.

3. Aussätze mit 2-Resultaten

Einige unsicheren Aussätze sind schon berührt worden, nämlich diejenigen, die eine grosse Anzahl Wiederfänge bei den Probefängen im ersten Herbst gegeben haben, wo aber im darauffolgenden Winter totaler O₂-Mangel vermutlich das Überleben verhindert hat. Streng genommen kann man in einem solchen Fall nicht von einem guten Resultat sprechen. Dass diese Aussätze trotzdem in der 2-Gruppe geführt wurden, beruht darauf, dass solche Seen unter gewissen Verhältnissen als eine Art Aufzuchtteiche für einsömmerige Fischjungen ausgenützt werden können. Das ist besonders der Fall bei sehr flachen, nicht allzu vegetationsreichen Seen, wo es möglich ist im Herbst mit

einfachen Fischgeräten eine grössere Anzahl Fische zu erhalten, um diese für Aussätze in anderen Seen verwenden zu können.

Abgesehen von diesen Fällen haben sämtliche unter der 2-Gruppe geführten Aussätze Wiederfänge mindestens 2 Jahre hindurch, am häufigsten aber mehrere und manchmal 10—12 Jahre hindurch gegeben. Vor allem wurden solche günstigen Resultate in fischleeren Seen mit verhältnismässig guten O₂-Verhältnissen erhalten. Es ist in diesem Zusammenhang recht interessant Fig. 2 mit Fig. 29 mit besonderer Markierung der fischleeren Seen zu vergleichen. Bei der Mehrzahl dieser Seen braucht man wahrscheinlich nicht einmal während langdauernder Winter mit O₂-Mangel zu rechnen (siehe Fig. 5—7). Die Ursache zu fischleeren Seen beruht auf Verhältnissen, die im vorangehenden Teil eingehend behandelt wurden (ALM l.c.), und auch hier schon berührt worden sind (Seite 56). In einigen dieser Seen mit guten Aussatzresultaten trat indessen, soweit man beurteilen kann, zufälligerweise so niedriger O₂-Gehalt auf, dass die ausgesetzten Fische untertauchten. Dies gilt für den Ö. Vontjärn und den Ilvåstjärn in den Wintern 1940—42 und vermutlich auch 1954—55.

Aussätze mit 2-Resultaten wurden sowohl mit Brut als auch mit einjährigen und älteren Jungen ausgeführt. Das erstere gilt z.B. Seeforelle im Hundtjärn D 70, Saibling-Kreuzungen im Nissetjärn C 215, Svarttjärn C 279, St. Hälltjärn C 278 und L. Hälltjärn C 277, Forellen-Kreuzungen im Nissetjärn, Coregonen und Coregonen-Kreuzungen im Ö. Vontjärn D 73, Grästjärn D 69, Ilvåstjärn D 33, Svarttjärn, Hundtjärn, Svarttjärn Bräcke u.a. Exempel für Aussätze von einjährigen Jungen mit reichem Resultat, sind die Bachforelle im Grästjärn und im Stockbergstjärn, Forellen-Kreuzungen im Ö. Gravtjärn C 198, Saibling im Grästjärn und V. Rörtjärn C 157, Saibling × Bachsaibling im Nissetjärn, L. Holmtjärn C 162 und L. Hälltjärn B, C 277. Es soll daran erinnert werden, dass der Aussatz im L. Holmtjärn, wie auch der mit zweijährigem Bachsaibling im Abborrtjärn 3 D 123 kein Resultat in diesen Seen gegeben hat, vielmehr in deren Abflussbächen und im letzteren Fall sogar in einem anderen See, in dem Abborrtjärn 1 D 126. Hier haben wir auch ein Exempel dafür, dass sich selbsterneuende feste Bestände gebildet haben. Im Übrigen war das nur mit Aussätzen von Barsch, Plötze, Elritze und Karausche sicher der Fall. Wie auf Seite 34 hervorgehoben ist ausserdem möglich dass ein gewisses Resultat beim Laichen der Coregonen im Grästjärn zustande gekommen ist. Ein fester Bestand ist aber dort nicht entstanden.

Gute Resultate wurden, wie oben angeführt, auch in Seen mit schon vorhandenem Barsch erhalten, aber gewöhnlich nur, wo grössere Junge der neuen Art ausgesetzt wurden. Mehrere Exempel hierfür sind ebenfalls schon angeführt worden auf Seite 59. Auch wenn es sich dabei in vielen Fällen um eine ziemlich geringe Anzahl ausgesetzter Exemplare handelt, war der Wiederfang doch manchmal recht hoch. In Tabelle 14 wurden sämtliche geglückte Aussätze solcher grösseren Jungen zusammen geführt und auch der

Tabelle 14. Zahl und % der Wiederfänge gewisser Aussätze.

Fischart	See	Alter bei Aussetzung	Zahl		% wiedergef.
			ausges.	wiedergef.	
Bachforelle	Stockbergstjärn	1	150	21	14,0
"	Grästjärn	1	600	28	4,7
Seeforelle	Hundtjärn	1	1.000	95	9,5
Bach-×Seeforelle	Ö. Gravtjärn	1	485	54	11,1
Saibling	Grästjärn D 69	1	740	126	17,0
"	V. Rörtjärn C 279	1	560	122	21,8
Bachsaiibling	Nissetjärn	1	150	46	30,7
"	" "	1	350	35	10,0
"	Ö. Vontjärn	1	300	43	14,3
Saibling×Bachsaiibling ..	L. Hälltjärn B	1	120	17	14,1
Bachforelle	Grästjärn	2	150	74	49,3
"	Libergstjärn	2	60	29	48,4
Seeforelle	S. Kyrktjärn	2	90	30	33,3
Äsche	Ö. Vontjärn	2	170	18	10,6
Bachforelle	Ö. Vontjärn	3	80	35	43,8
Seeforelle	" "	3	100	33	33,0
Meerforelle	Storörmyrtjärn	4	48	15	31,3
Coregonen	Grästjärn	4	80	41	50,1
"	Ilvästjärn	4	32	23	72,0
"	Abborrtjärn 2	?	600	77	12,8

erhaltene Wiederfang in Prozenten. Abgesehen von der Raubfischerei sind bei zweijährige und ältere Fische oft 50 %, zuweilen noch mehr wiedergefangen worden und bei einjährigen Jungen hat sich der Wiederfang gewöhnlich zwischen 10 und 20 % gehalten. Auch einzelne Brutaussätze haben, wie aus den Tabellen hervorgeht, einen sehr hohen Wiederfang ergeben, auch wenn die Ziffern für die Anzahl der ausgesetzten Brut selbstverständlich ziemlich unsicher sind. Das beste Resultat würde in diesem Fall der Ö. Gravtjärn C 198 aufzeigen. Von 2.000 Brut einer Coregonen-Kreuzung gaben die Wiederfänge in den folgenden Jahren zusammen 540 Stück, was 27 % entspricht.

4. Vergleich von Seen mit 2-Resultaten

Aus dem Bericht in Kapitel III über die Aussatzresultate der verschiedenen Fischarten geht hervor, dass die als geglückt bezeichneten Aussätze ziemlich verschiedenen Grades waren. Einige haben besonders gute Wiederfänge was Anzahl und auch Gewicht betrifft gegeben. Andere haben vielleicht eine verhältnismässig grosse Anzahl Fische gegeben, aber mit schlechter Zuwachs, was ein niederes Totalgewicht zur Folge hatte. Schliesslich waren gewisse Aussätze, trotzdem sie innerhalb dem Rahmen der 2-Gruppe lagen, ziemlich schlecht was Anzahl und Gewicht betraf.

Weiter ging hervor, dass Aussätze verschiedener Fischarten im selben See in mehreren Fällen sehr gute Resultate gegeben haben. Als Exempel hierfür

Tabelle 15. Im See Grästjärn D 69 wiedergefangenen Fische.

Jahr	Bachforelle		See-forelle		Lachs		Saibling		Coregonus ?		Coregonus „Smerling“ X „Storsik“		Sämtl.	
	Zahl	Gew.	Z.	G.	Z.	G.	Z.	G.	Z.	G.	Z.	G.	Z.	G.
1936	26	1,3	—	—	—	—	—	—	27	6,4	—	—	53	7,7
37	29	9,0	—	—	—	—	—	—	2	1,5	—	—	31	10,5
38	13	5,7	—	—	—	—	—	—	3	3,0	—	—	16	8,7
39	6	3,6	—	—	—	—	—	—	2	3,1	—	—	8	6,7
40	—	—	—	—	—	—	—	—	6	11,7	—	—	6	11,7
41	—	—	—	—	—	—	—	55	4,0	4	1,0	—	59	5,0
42	—	—	—	—	—	—	—	17	2,1	9	6,1	—	26	8,2
43	—	—	—	—	—	—	—	24	5,3	3	2,2	—	27	7,5
44	—	—	2	0,1	—	—	—	12	4,7	4	4,0	—	18	8,8
45	—	—	4	1,0	—	—	—	7	5,2	1	1,5	—	12	7,7
46	—	—	—	—	—	—	—	2	2,2	1	1,7	—	3	3,9
47	—	—	2	2,2	—	—	—	2	2,9	1	2,6	—	5	7,7
48	—	—	—	—	—	—	—	—	—	3	8,5	—	3	8,5
49	—	—	4	2,0	—	—	—	7	5,2	1	1,5	—	12	8,7
50	—	—	—	—	6	0,6	—	—	—	—	—	—	6	0,6
51	—	—	—	—	—	—	—	—	—	—	—	—	—	—
52	18	1,7	—	—	1	0,5	—	—	—	—	36	1,0	55	3,2
53	8	2,4	—	—	—	—	—	—	—	—	174	23,6	182	26,0
54	1	0,5	—	—	—	—	—	—	—	—	80	26,1	81	26,6
55	1	0,7	—	—	—	—	—	—	—	—	52	2,1	53	2,8
56	—	—	—	—	—	—	—	—	—	—	84	5,9	84	5,9
57	—	—	—	—	—	—	—	—	—	—	41	2,7	41	2,7
58	—	—	—	—	—	—	—	—	—	—	71	5,1	71	5,1
59	—	—	—	—	—	—	—	—	—	—	38	2,1	38	2,1
1960	—	—	—	—	—	—	—	—	—	—	45	2,5	45	2,5
Sämtl.	102	24,9	12	5,3	7	1,1	126	31,6	67	54,8	621	71,1	935	188,8

können vor allem Grästjärn und Ö. Vontjärn genannt werden, aber auch Hundtjärn, Nissetjärn und Ö. Gravtjärn. Um diese Tatsache näher beleuchten zu können, wurden die Resultate der in den beiden erstgenannten Seen gemachten Aussätze in den Tabellen 15 und 16 zusammengestellt. Der Totalertrag im Grästjärn betrug im Verlauf von 25 Jahren 935 Fische mit einem gemeinsamen Gewicht von 189 kg und im Vontjärn im Verlauf von 24 Jahren 703 Fische von 238 kg, was gleichbedeutend ist mit 7,5 bzw. 9,9 kg per Jahr.

Es ist von Interesse aus diesen Ziffern, wie auch aus denen der übrigen Seen mit Aussätzen die 2-Resultate zu verzeichnen hatten, den jährlichen Hektarertrag zu errechnen. In Tabelle 17 wurde hierüber eine Zusammenstellung gemacht. Die Seen sind dort nach der Grösse der Hektarerträge geordnet. Dabei findet man, dass der Ertrag der Mehrzahl der Seen ungefähr 1 kg beträgt, mit etwa gleich vielen Seen über wie unter dieser Ziffer liegend. Weiter wird deutlich, dass Seen mit hohen sowie niederen Hektarerträgen innerhalb der in meiner früheren Arbeit aus limnologischen Gesichtspunkten aufgestellten verschiedenen Gruppen fallen (siehe Tabelle 1). Besonders muss hervorgehoben werden, dass drei Seen mit den höchsten Hektarerträgen unter Gruppe I fallen. Dies gilt dem Grästjärn mit 3,8 kg, dem Ö. Vontjärn mit

Tabelle 16. Im See Ö. Vontjärn D 73 wiedergefangenen Fische.

Jahr	Bachforelle		Seeforelle		Bachsaibling		Regenbogenforelle		Äsche		Coregonus „Aspsik“		„Bläsik“ „Smerling“		Kleine Maräne „Storsik“		Sämtl.	
	Zahl	Gew.	Z.	G.	Z.	G.	Z.	G.	Z.	G.	Z.	G.	Z.	G.	Z.	G.	Z.	G.
1937	25	5,5	19	4,4	—	—	—	—	—	—	—	—	—	—	—	—	44	9,9
38	6	3,1	9	6,6	—	—	—	—	—	—	—	—	—	—	—	—	15	9,7
39	4	5,9	4	5,5	—	—	—	—	—	—	—	—	—	—	—	—	8	11,4
40	—	—	1	1,8	—	—	—	—	—	—	—	—	—	—	—	—	1	1,8
41	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
42	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
43	—	—	—	—	—	—	1 ¹	0,4	—	—	—	—	—	—	—	—	1	0,4
44	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
45	—	—	—	—	26	4,9	—	—	—	—	10	0,6	—	—	—	—	36	5,5
46	—	—	—	—	17	10,5	—	—	—	—	75	25,7	—	—	—	—	92	36,2
47	—	—	—	—	—	—	—	—	—	—	33	26,4	—	—	—	—	33	26,4
48	—	—	—	—	—	—	—	—	—	—	22	30,0	—	—	—	—	22	30,0
49	—	—	—	—	—	—	—	—	17	3,0	8	12,9	—	—	—	—	25	15,9
50	—	—	—	—	—	—	—	—	1	0,4	4	7,6	—	—	—	—	5	8,0
51	—	—	—	—	—	—	—	—	—	—	2	4,2	—	—	—	—	2	4,2
52	—	—	—	—	—	—	—	—	—	—	1	2,2	—	—	—	—	1	2,2
53	—	—	—	—	—	—	—	—	—	—	—	—	24	0,6	—	—	24	0,6
54	—	—	—	—	—	—	—	—	—	—	—	—	23	2,4	—	—	23	2,4
55	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
56	—	—	—	—	—	—	12	0,1	—	—	—	—	—	—	—	—	12	0,1
57	—	—	—	—	—	—	7	1,5	—	—	—	—	—	—	12	0,4	19	1,9
58	—	—	—	—	—	—	5	2,7	—	—	—	—	—	—	70	6,6	75	9,3
59	—	—	—	—	—	—	—	—	—	—	—	—	—	—	136	28,1	136	28,1
1960	—	—	—	—	—	—	—	—	—	—	—	—	—	—	129	34,4	129	34,4
Sämtl.	35	14,5	33	18,3	43	15,4	25	4,7	18	3,4	155	109,6	47	3,0	347	69,5	703	238,4

¹ Ausgesetzt 42, im Frühl. Brut 1.000.

3,3 kg und dem Hundtjärn mit 8,6 kg per ha. Sämtliche sind mehr oder weniger ausgeprägt dystrofe Seen und von dem Typ, den man oft als ungeeignet für Salmoniden und Coregonen betrachtet, ausserdem als weniger ertragreich was das Produktionsvermögen und den Fischertrag betrifft. Es scheint deshalb angebracht, hier einige Daten über diese Seen anzugeben.

Grästjärn und Vontjärn sind hochbelegene Endseen, der Vontjärn ist ganz von Wald- und Moränengebieten umgeben, der Grästjärn grösstenteils von Mooren (Taf. 1). Der Vontjärn hat deshalb hauptsächlich feste Ufer. Nur ein kleines Gebiet im westlichen Teil des Grästjärn ist teilweise steinig und mit Felsenuffern. Der Hundtjärn liegt in der Nähe des Grästjärn und ist ein Sickersee ganz von Mooren umgeben. Die grösste Tiefe ist im Grästjärn 4,5 m, im Vontjärn 4 m und im Hundtjärn 3 m. Die Seefarbe ist in sämtlichen Seen gelbbraun bis braun, die Transparenz im Grästjärn 1,6 m, im Vontjärn 1,8 m und im Hundtjärn 2,0 m. Das pH beträgt im Durchschnitt 5,9 resp. 6,3 und 5,8, die Alkalinität 0,09—0,20 resp. 0,17 und 0,21—0,24 und das Leitvermögen 24,5 resp. 29,9, im Hundtjärn nicht untersucht. Die Seen gehören demnach den polyhumosen, dystrophen Typen an. Die Temperatur- und

IX. Erklärungen zu den Tafeln

In sämtlichen hier aufgenommenen Seen haben Aussätze einer oder mehreren Fischarten gute Resultate gegeben (vergl. Tab. 1: 15 u. 16).

Foto Verf., mit Ausnahme I: 1 und III: 1, 2 G. Molin.

Tafel I.

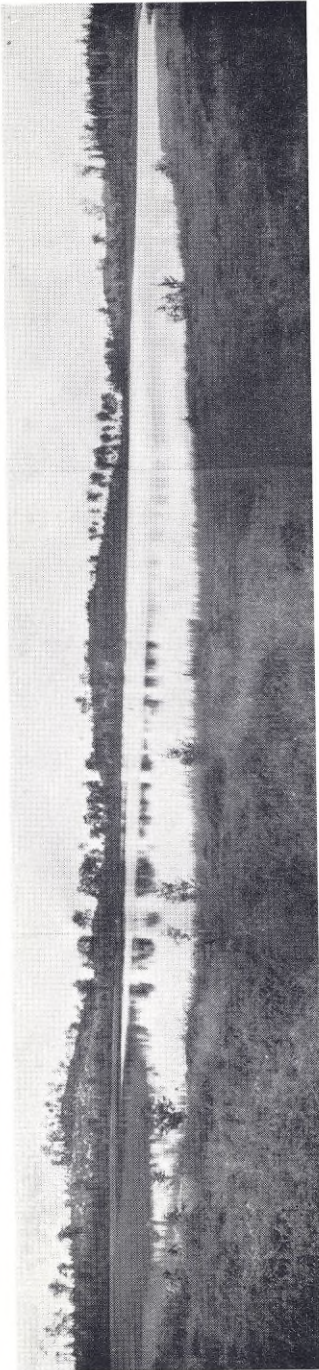
1. Ö. Vontjärn D 73. Fischleer. Hauptsächlich Moränenboden mit Steinufern, von Wald umgeben. 2. Grästjärn D 69. Fischleer. Nordw. Teil. Meist versumpfte Umgebungen mit Carex-Wuchs. Anwendung des grösseren Schlauchbootes. 3. Der gleiche See, südl. Teil mit grossen Schwingrasen, gesehen von einem Hügel am Ufer.

Tafel II.

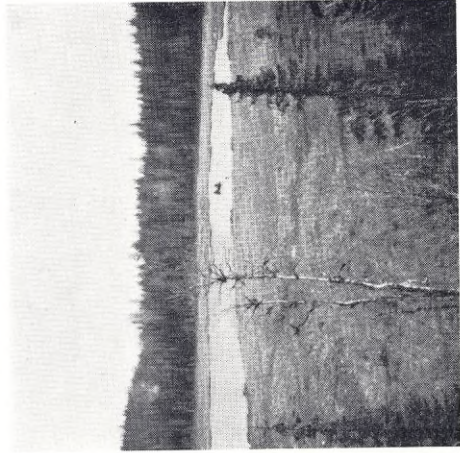
1. Barntjärn B 118. Fischleer. Östl. Teil mit typischem Schwingrasenufer. 2. Libergstjärn C 228. Fischleer. Carex-Wiese. Probefang mit dem kleineren Schlauchboot. 3. Nissetjärn C 215. Fischleer. Nord-w. Teil. Hauptsächlich steinige bewaldete Ufer. 4. Abborrtjärn 2 D 125. Barsch und Hecht. Nord-w. Teil. Schwingrasen mit Carex, dann jäh abfallend. 5. Der gleiche See, nord-ö. Teil mit festem, langsam abfallendem Ufer.

Tafel III.

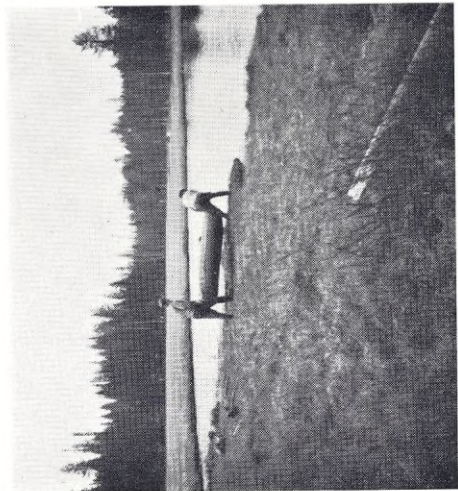
1. Stockbergstjärn A 106. Elritze. Hauptsächlich feste Ufer. 2. S. Kyrktjärn C 209. Barsch. Nord-ö. Teil, abwechselnd feste und lose Ufer. 3. Lejonrostjärn C 205. Nord-w. Teil. Ufer wie beim Kyrktjärn.



1.



3.



2.



1.



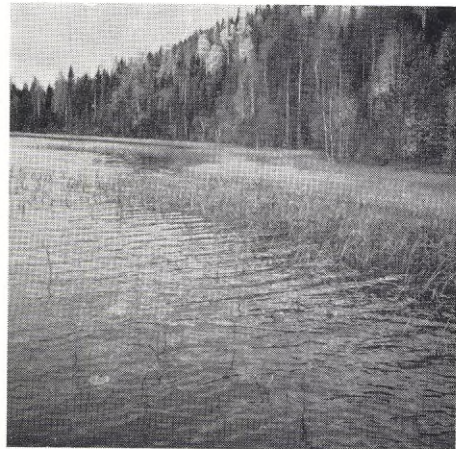
2.



3.



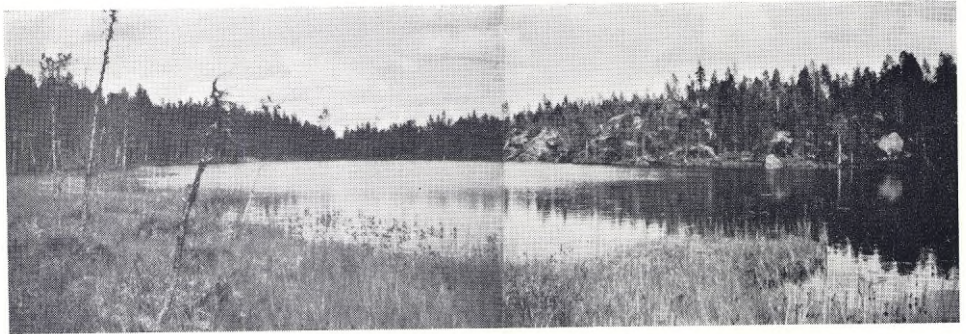
4.



5.



1.



2.



3.

Tabelle 17. Jahres- und Hektar-Erträge in den Seen mit 2-Resultaten. (Die Ertragszahlen gelten nur für die ausgesetzten Fischarten.)

See	Grösse in ha	Tiefe m.	Ausgesetzte Fischarten ¹	Zahl der Jahre der Probe- fänge	Fangerträge in kg.		
					Gesamt	Pro Jahr	Pro Jahr und ha
Hundtjärn D 70 . . .	1,0	3,0	Sf, C×Km	8	68,8	8,6	8,6
Grästjärn D 69 . . .	2,0	4,5	L, Bf, Sf, S, C, C×C	25	188,8	7,5	3,8
Ö. Vontjärn D 73 . . .	3,0	4,0	Bf, Sf, Bs, R, Ä, C C×C, C×Km	24	238,4	9,9	3,3
Svarttjärn, Bräcke	2,0	7,5	C	7	47,3	6,8	3,4
Ö. Gravtjärn C 198	2,5	7,0	Mf×Bf, C×Km	12	61,0	5,1	2,0
Nissetjärn C 215 . .	1,5	8,0	Bf×Sf, Bs, S×Bs	14	43,4	3,1	2,0
Libergstjärn C 228	0,5	2,0	L, Bf	4	3,6	0,9	1,8
Stockbergstj. A 106	2,0	5,0	Bf	2	5,7	2,9	1,5
La. Hältj. B C 277	0,5	?	S	4	2,8	0,7	1,4
Bodtjärn D 68	1,5	4,0	B	6	11,6	1,9	1,3
Långsmaltj. C 49 . .	3,0	?	C, C+C	8	24,4	3,9	1,3
St. Hältj. C 278 . . .	3,0	5,0	S×Bs	2	6,9	3,5	1,2
Svarttjärn C 279 . . .	8,0	3,5	S×Bs, C	8	67,3	8,4	1,1
La. Hältj. C 277 . . .	1,5	2,0	S×Bf	4	6,1	1,5	1,0
Kyrktj. S C 209 . . .	1,0	4,5	Bf, Sf, C	11	11,3	1,0	1,0
V. Rörtjärn C 157 . .	5,5	5,0	S, C×C	14	68,9	4,9	0,9
Ilvåstjärn D 33 . . .	2,0	9,0	C	12	20,2	1,7	0,9
Abborrtj. 1 D 126 . .	2,0	8,0	C×C	4	4,1	1,2	0,6
Abborrtj. 2 D 125 . .	6,5	11,0	C	11	32,0	3,0	0,5
Lugnsjöjtj. D 127 . .	1,5	4,5	C	1	0,6	0,6	0,4
Dracksjön C 296 . . .	19,0	6,5	C×Km	3	21,5	7,1	0,4
Storörmyrtj. C 160	7,5	17,0	Mf	5	13,6	2,7	0,4
Abborrtj. 3 D 123 . .	2,5	6,5	Bs	8	6,7	0,8	0,3
Lillsjön D 67	16,0	3,0	A	7	37,2	5,3	0,3
Tjärn A 110	3,5	?	C×Km	1	0,5	0,5	0,14
Svarttjärn D 120 . . .	13,0	11,0	A	12	20,9	1,8	0,14

¹ Bezeichnungen wie in Tab. 1.

O₂-Verhältnisse (Fig. 4 u. 5) sind wie die übrigen Faktoren ziemlich gleich in den drei Seen. Der O₂ Gehalt im Vontjärn war doch im Winter 1941 niedriger als im Grästjärn, sicher trat damals, wie oben genannt, im Vontjärn totaler O₂-Mangel ein. Hierfür spricht auch die Tatsache, dass kein Fisch im Vontjärn in den Jahren 1941 und 1942 erhalten wurde (Tab. 16), was dagegen im Grästjärn der Fall war (Tab. 15).

Der Vontjärn besitzt eine ziemlich reiche Vegetation an Wasserrosen, *Potamogeton*, *Myriophyllum*, *Characeen* und Wassermoosen. Im Grästjärn und Hundtjärn ist die Vegetation recht sparsam. In der Fauna des Grästjärn und des Vontjärn kommen reichlich *Chironomiden* und *Pisidium*, im Vontjärn ausserdem *Corethra* vor. Die Fauna des Hundtjärn ist nicht untersucht.

Mehrere der übrigen Seen mit 2-Resultat zeigen limnologisch gesehen grosse Ähnlichkeit mit den eben berührten. Die Tafel II—III zeigen einige dieser Seen mit ihrer nächsten Umgebung. Es ist sehr wahrscheinlich, dass wenn mehrere Aussätze, und von verschiedenen Fischarten, gemacht worden sind, in diesen Seen bedeutend höhere Fang- und Hektarziffern hätten erhalten werden können, als dies wirklich der Fall war. Dasselbe gilt, wenn der Fang

intensiver betrieben und die Aussätze öfter gemacht worden wären. Es soll auch daran erinnert werden, dass sich in mehreren Seen Fischbestände befinden, von denen sicher noch durch Jahre hindurch grössere oder kleinere Fänge erwartet werden können (S. 83). Dazu kommt, dass sich in einigen Seen, besonders in solchen mit niederem Hektarertrag, ausser den Fischen die in die Versuche eingingen, noch andere Fischarten befunden haben. Dies gilt in erster Linie für Barsch, in einigen der Seen auch für Hecht, Plötze und Quappe. Sofern man den Fang auch auf diese Arten konzentriert und sie mitgerechnet hätte, wäre natürlich der Wiederfang reicher ausgefallen. Noch mehr gilt das für viele Seen in denen Raubfang getrieben wurde. Vermutlich wurden dabei in vielen Fällen mehr Fische gefangen, als durch die Probefänge erhalten wurden. Die in Tab. 17 aufgenommenen Ziffern sagen deshalb recht wenig über die bestmöglichen Fischerträge und die wirkliche Produktion respektiver Seen. Beides liegt vermutlich bedeutend höher als die in die Tabellen aufgenommenen Ziffern angeben.

In dem Mass als dieses Ertragsvermögen mit dem Nahrungszugang zusammenhängt, kann hier hervorgehoben werden, dass der Reichtum der Litoral- und Profundalfauna in den Seen, die Gegenstand der Untersuchungen hierüber waren, keinen grösseren Unterschied in den daselbst aufgestellten Seetypen gezeigt hat (ALM 1960). Folglich sind hohen und niederen Werte was Anzahl und Gewicht dieser Fauna betrifft, erhalten worden sowohl in den stark polyhumosen als auch in den harmonisch oligotrophen Seen. Doch entsprechen diese Werte nicht direkt der für die Fische erreichbaren Nahrungsmenge. Diese beruht nämlich in hohem Grade auf der Morfometri der Seen, welche eine grosse Einwirkung auf die Fauna sowie auf die Temperatur- und O_2 -Verhältnisse hat. Frühere Untersuchungen haben gezeigt, dass die Bodenfauna der Profundal meistens ärmer ausgebildet ist als die Litoralfauna. Weiter darf man in kleinen Seen, wie die betreffenden Typen, oft im Sommer mit niedrerem O_2 -Gehalt in der Hypolimnion rechnen, je tiefer der See ist. Besonders in vielen kleinen aber gleichzeitig tiefen Seen, bekommt deshalb die nahrungsreiche Litoralregion, verhältnismässig gesehen, ein geringeres Ausmass, und die tieferen Wasserschichten können für die Fische ungeeignet werden. Die Gesamtproduktion der für die Fische erreichbaren Nahrung wird so ziemlich klein. Die weniger tiefen Seen er bieten hier, vorausgesetzt dass der O_2 -Gehalt genügend ist, bedeutend günstigere Voraussetzungen. Als Exempel hierfür kann der Ö. Vontjärn und der Ilvåstjärn angeführt werden. Figur 28 zeigt die Tiefenverhältnisse in diesen und einigen anderen Seen von verschiedenen morfometrischen Typus. Wie daraus ersichtlich ist, zeigt besonders der Vontjärn aber auch der Hundtjärn und Grästjärn eine bedeutend grössere Litoralregion bis zu 3 u. 4 m Tiefe als der Ilvåstjärn, in dem diese Region bedeutend schmaler ist im Verhältnis zum ganzen Areal. Leider sind die Tiefenverhältnisse nicht so detailliert bekannt von den anderen Seen mit niederem Hektarertrag, dass Niveaukurven hätten gemacht wer-

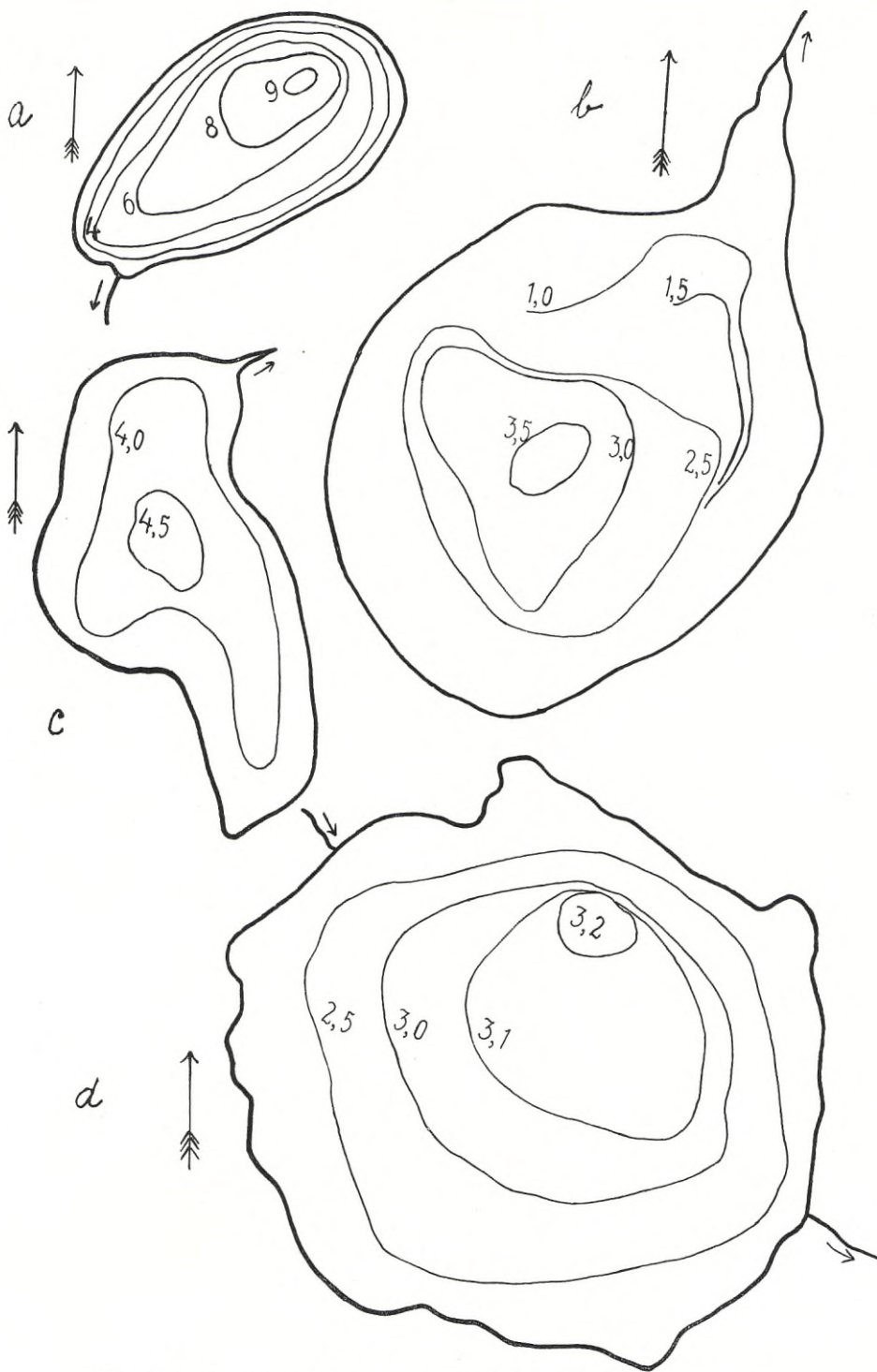


Fig. 28. Die Morphometrie einiger Kälarne-Seen. (Masstab verschieden.)
 a) Ilvåstjärn D 33; b) Ö. Vontjärn D 73; c) Grästjärn D 69; d) Hundtjärn D 70.

den können. Es wurde schon hervorgehoben, dass der Zuwachs bei den Coregonen im Ilvåstjärn schlecht war verglichen mit dem Vontjärn und Grästjärn. Gleichzeitig waren auch die Hektarerträge im Ilvåstjärn ungewöhnlich nieder. Grössere Unterschiede liegen indessen nicht vor in diesen Seen, was Transparenz, pH, Alkalinität und Leitvermögen betrifft. Für den Vontjärn sind die betreffenden Ziffern oben angegeben. Im Ilvåstjärn war Transparenz 1,8 m, pH Wert 6,3 samt Alkalinität und Leitvermögen 0,22 resp. 30,6. Die Ursache zu den Unterschieden im Zuwachs und Ertrag muss deshalb anderswo gesucht werden. Es ist anzunehmen, dass der wahre Grund dazu die unterschiedliche Morfometri der eben genannten Seen und deren Einfluss auf die Temperatur- und O₂-Verhältnisse ist. Der Ilvåstjärn mit seinen steilen Ufern und einer Tiefe von 9 m zeigt im Sommer eine ausgeprägte Schichtung der Temperatur- und O₂-Gehalt (Fig. 4), mit nur 3 mg/l O₂ schon in 2 m Tiefe. Der See ist ein Sickersee, wahrscheinlich von meromiktischem Typus, und hat im Sommer wie im Winter wie schon genannt sehr geringen O₂-Gehalt bisweilen totalen O₂-Mangel. Im Ö. Vontjärn dagegen mit seinen weitabfallenden, teilweise flachen Ufern ist im Sommer der O₂-Gehalt in 2 m Tiefe 7—8 mg/l und in 3 m Tiefe variierte dieser während verschiedener Jahre zwischen 3 und nahezu 8 mg/l. Wie oben hervorgehoben, ist aber vermutlich im Winter gewisser Jahre O₂-Mangel im Vontjärn eingetreten. Es ist doch offensichtlich, dass die Unterschiede in den O₂-Gehalt im Sommer im Zusammenhang mit der breiteren Litoralzone und den Tiefenverhältnissen machen, dass die für Fische normal zugängliche Nahrungszone im Ilvåstjärn weit geringer ist als im Vontjärn.

Dazu kommt, dass der Ilvåstjärn äusserst arm an Vegetation ist. Der Zugang zu *Chironomus*-Arten war auch hier weit geringer als im Vontjärn (ALM 1960). Dagegen kommt im Ilvåstjärn *Sphaerium* besonders reichlich vor. SVÄRDSON (1950) fand im grossen und ganzen dieselben Organismen in der Nahrung der Coregonen in beiden Seen, nämlich verschiedene Tiere die der Litoralfauna zugehören, im Ilvåstjärn ausserdem etwas Plankton.

Ein Überblick über die in Tabelle 17 aufgenommene Grösse und Tiefe der Seen zeigt doch keinen solchen allgemeinen Zusammenhang zwischen Tiefe und Hektarertrag wie eben vom Vontjärn und Ilvåstjärn angezeigt wurde. Doch wird deutlich, dass die übrigen Seen mit hohem Hektarertrag, besonders der Grästjärn und der Hundtjärn nicht besonders tief sind. Aber auch unter Seen mit niederem Hektarertrag trifft man solche mit geringer Tiefe. Wahrscheinlich sind es die O₂-Verhältnisse samt in einigen Fällen Konkurrenz und Prädation der schon vorhandenen wie auch neuangesetzten Arten, was hier hereinspielt. Der geringe Spielraum und das Fehlen nötiger Nischen für mehrere Fischarten, müssen in den kleinen Seen, von denen hier die Rede ist, notwendigerweise wichtige die Produktion begrenzende Faktoren sein.

Die oben berührten geglückten Resultate von Aussätzen verschiedener Lachsfische zeigen inzwischen deutlich, dass die hydrographischen und che-

mischen Faktoren von recht untergeordneter Bedeutung auch für diese Arten sind. Sowohl Forellen als auch Coregonen verschiedener Formen und Bachsaibling haben was die Wiederfänge und den Zuwachs betrifft in einer Mehrzahl Seen von ausgesprochen dystrophem Typus ausgezeichnete Resultate gegeben. Auch Saibling, der ja oft als einer der meist fordernden Fischarten betrachtet wird, ist gut gelungen in einigen dieser Seen. Es soll doch betont werden, dass die zwei Seen die von Anfang an Saibling hatten, nämlich der Storörmyrtjärn C 160 und der Ö. Rörtjärn C 158 nicht von ausgesprochen dystrophem Typus waren, besonders der Ö. Rörtjärn nicht. Sie zeigten gute O₂-Verhältnisse, der Rörtjärn ausserdem hohe Transparenz von 4,9 m und grüne Seefarbe, während der pH Wert nur 6,9 erreichte. Im Storörmyrtjärn war die Transparenz nur 2,6 m und der pH Wert 6,4. Indessen waren bei diesen beiden Seen die Ufer teilweise härter mit Stein und Sand, was das Laichen und die seit langer Zeit bestehenden festen Bestände möglich machte. Diese Bestände werden schon im 18. Jahrhundert von HÜLPHERS (1775/1912) genannt. Dass der Saibling später zurückging beruht sicher auf den vorher genannten unglücklichen Aussätzen von Barsch und Plötze im Storörmyrtjärn und von Elritze im Ö. Rörtjärn, die von der Bevölkerung ausgeführt wurden.

Auch wenn Lachsfische ausgesetzt werden können und sich gut halten in den nun berührten Kleinseen verschiedener Typen, muss man doch damit rechnen, dass eine natürliche Vermehrung nicht zustande kommen kann. Abgesehen von den zwei eben genannten ursprünglichen Saiblingseen, den unsicheren Fall mit Coregonen im Grästjärn und den beiden Fällen mit festen Bachsaibling-Beständen in den Abflussbächen des L. Holmtjärn und des Abborrtjärn 1, konnte keine Reproduktion konstatiert werden. Diese ausgebliebenen Laichresultate beruhen selbstverständlich bei der Mehrzahl der Seen in erster Linie auf dem Mangel an geeigneten Laichböden. Die Stimulans, die nach FABRICUS (1950) zur Auslösung des Laichen erforderlich ist, ist möglicherweise nicht vorhanden gewesen. Doch war dies kein Hindernis für die Entwicklung normaler Geschlechtsprodukte. Meistens haben nämlich die gefangenen Fische bei erreichter Reife Rogen und Milch gehabt. Auch sind diese Geschlechtsprodukte, abgesehen von gewissen Ausnahmen, oft mit gutem Resultat für künstliche Befruchtung und weitere Erbrütung angewendet worden.

In einigen Seen, in denen sich einigermassen geeignete Laichböden befanden, haben die Fische vermutlich gelaicht, da dort Laichgrube beobachtet werden konnten. Es ist dann möglich dass Rogen und Brut aufgefressen wurden, oder aber war die Befruchtung gewisse Kreuzungen betreffend, schlecht ausgefallen. Möglich ist auch, dass der niedere pH Wert in gewissen Fällen die Befruchtung verhindert oder erschwert hat. Was die Forellen betrifft, hat DAHL gezeigt (1926), dass dieser Umstand eintreten kann bei einem pH-Wert der unter 5,5 liegt. So niedere Werte sind aber nur in ganz vereinzelt Fällen in den Kälarne-Seen erhalten worden. In diesem Zusammenhang kann

angeführt werden, dass das Auslegen grosser Mengen von Sand und Kies in gewissen ähnlichen Kleinseen bei Kloten das Laichen der dort ausgesetzten Bachsaiblingen (ALM 1921) ermöglicht hat. Das Resultat fiel aber schlecht aus, und nur eine geringe Anzahl Fische einer neuen Generation wurden gefangen.

V. Fischertrag aus früher fischführenden Kälarne-Seen

Zur Komplettierung des Berichts auf den letzten Seiten, der den Ertrag hauptsächlich fischleerer Seen mit geglückten Fischaussätzen behandelt, schien es mir von Interesse hier einige Angaben mit hereinzunehmen, die im Zusammenhang mit den limnologischen Untersuchungen der Kälarne-Seen über die Fischerträge einiger ursprünglich fischführenden Seen eingeholt wurden. Diese Angaben wurden von den zuständigen Fischmeistern beschaffen vom Jahr 1939 und aufs Neue zur Kontrolle 1950, und sind nun in Tabelle 18 eingetragen worden. Die Seen wurden dort in die 4 verschiedenen limnologischen Gruppen aufgenommen und ausserdem innerhalb jeder Gruppe nach der Tiefe geordnet. Die Lage der Seen geht aus Figur 1 und die daselbst schon vorhandenen Fischarten auch aus Figur 29 hervor.

Wie ersichtlich ist, liegen Angaben vor über Kleinseen, viele schon im Zusammenhang mit mehr oder weniger missglückten Aussätze berührt, wie auch von grösseren Seen. Weiter geht daraus hervor, dass die Angaben aus den beiden Zeitabschnitten in oft hohem Grade divergieren. Es sind dann gewöhnlich die letzten Ziffern bedeutend niedriger. Angaben über gewisse Seen von 1939 scheinen im Vergleich unnatürlich hoch, z.B. Mörtsjötjärn, Bodflotjärn, Gårdtjärn, Gäddtjärn, Loktjärn u.a. Manchmal liegen dagegen die Angaben von 1950 höher als die von 1939. Das ist besonders der Fall von einigen der grösseren, seltener von den kleineren Seen. Trotz dieser ziemlich unsicheren Ziffern, wurden in der Tabelle die Angaben von 1939 und 1950 zusammengeschlagen und vom Mittel der Hektarertrag ausgerechnet. Dieser variiert bei diesen 54 Seen zwischen 1,5 und 15,0 kg wie folgt: 5 Seen < 2,0 kg, 22 Seen 2,1—5 kg, 17 Seen 5—10 kg und 10 Seen 10—15 kg. Für sämtliche Seen ist das Mittel 6,2 kg.

Frühere Angaben über die Hektarerträge der schwedischen Seen finden sich in Werken von CEDERSTRÖM-TIBERG (1895), O. NORDQUIST (1918) und ALM (1936). Tiberg kam bei 30 Seen in der Provinz Värmland zu einem Mittel von 4,3 kg mit kleinsten und grössten Wert ca. 1,8 und 10 kg. Nordquist, der eine Statistik zusammengestellt hat von 192 hauptsächlich mittelgrossen und grossen Seen verschiedener Landesteile, (Primärangaben für die offizielle Fischereistatistik) hat für den Hauptpart dieser Seen einen Hektarertrag von 2—4 kg gefunden. Er macht weiter darauf aufmerksam, dass der Hektarertrag von flacheren (< 10 m) zu tieferen Seen und gleichzeitig von kleineren zu grösseren Seen abnimmt. Bei gewissen buchgeführten Seen, ver-

Tabelle 18. Jahres- und Hektar-Erträge in einigen Kälarne-Seen.

Gruppe	Name	Grösse in ha	Tiefe in m.	Fische ¹	Jahresertrag in kg				
					1940	1950	Mw.	Kg pro ha	
I	Mörtsjötjärn D 30	2	2	BHP	35	5	20	10,0	
	Flaskjärn D 75	4	4,5	BHPQA	6	5	6	1,5	
	Lönrostjärn C 166	5	4,5	B	60	—	60	12,0	
	Brantbergstjärn D 74	3	6,5	BHPQA	40	5	23	7,7	
	Bodflotjärn D 44	2,5	9	B	40	20	30	12,0	
	Per Sjulsonstjärn C 119	6	9	BF	30	5	18	3,0	
II	Ältjärn C 121	13	2	BHPQA	100	25	63	4,8	
	Flarken A 152	31	2,5	BHPQACEU	200	200	200	6,1	
	Skällsjön B 117	56	3	BHPQACEUBr	660	520	590	10,5	
	Kvarnsjön B 104	10	3	BHPQA	75	50	63	6,3	
	Gårdtjärn D 124	9,5	4	BHPQA	235	50	143	15,0	
	Gäddtjärn St. B 121	1,5	4	BHPQ	27	10	19	12,7	
	Lövsjön B 103	18	4	BHPQA	70	50	60	3,3	
	Loktjärn D 79	3,5	4	BHPQA	60	30	45	12,8	
	Nästjärn B 105	2	4,5	BHQA	25	15	20	10,0	
	Kyrktjärn Sö. C 209	1	4,5	B	6	—	6	6,0	
	Mannsjön B 106	14	5	BHPQAFCA	85	100	93	6,6	
	Lillsjön B 126	53	5	BHPQAC	200	250	225	4,3	
	Övsjön C 67	41	5	BHPQACE	400	350	375	9,1	
	Mörtsjön D 34	36	5,5	BHPQACE	200	100	150	4,2	
	Bodsjötjärn D 83	18	6	BHPQA	175	30	53	2,9	
	Kyrktjärn No. C 208	1	7,5	BF	10	—	10	10,0	
	Mjösjön D 121	62	8	BHPQAC	400	500	450	7,3	
	Lejonrostjärn C 205	1	8	C	6	—	6	6,0	
	Täckelsjön V. C 122	28	9	BHPQAC	115	150	133	4,7	
	Kolbjörnstjärn B 94	10,5	10	BPQ	15	—	15	1,4	
	Gastsjön C 66	140	9	BHPQACE	300	625	463	3,3	
	Abborrtjärn 2, D 125	6,5	11	BH	25	20	23	3,5	
	Storrörmyrtjärn C 160	7,5	17	S	45	10	28	3,7	
	III	Krångtjärn D 78	7	4	BHPQA	100	50	75	10,7
		Hongsjön B 123	41	4,5	BHPQAC BrEU	600	550	575	14,0
		Myrbärtjärn C 165	2	4,5	B	25	25	25	12,5
Kälsjön C 116		43	6	BHPQ	225	50	138	3,2	
Meckflotjärn St. B 119		6,5	6	BH	25	50	38	5,8	
Balsjön D 7		64	7	BHPQAF CÄBrEU	400	600	500	7,8	
Rörtjärn Ö. C 158		10	7,5	S	100	150	125	12,5	
Bodsjön D 82		70	8	BHPQAF CÄBrEU	325	230	278	4,0	
Gransjön D 8		50	8	BHPQAF CÄBrEU	250	300	275	5,5	
Täckelsjön Ö. C 164		125	9	BHPQAC	325	175	250	2,0	
Hemsjön A 177, B 89		350	9,5	BHPQACBrEU	350	2.800	1.575	7,3	
Singsjön B 124		640	10	BHPQACE	2.350	7.000	4.675	2,8	
Mellansjön C 168		150	11,5	BHPQACE	600	225	413	2,8	
Holmtjärn St. C 163		16	11,5	B	30	—	30	1,9	
Högtjärn D 36		8,5	12,5	BHPQA	90	30	60	7,1	
Lugnsjön D 119		350	14	BHPQAF CBrÄEU	600	1.000	800	2,3	
Hällesjön D 37		125	16,5	BHPQAF CBrÄEU	600	250	425	3,4	
Fisksjön B 90		420	23	BHPQAE	1.700	500	1.100	2,6	

¹ Bezeichnungen wie im Tab. 1.

Tabelle 18. Forts.

Gruppe	Name	Grösse in ha	Tiefe in m.	Fische ¹	Jahresertrag in kg			
					1940	1950	Mw.	Kg pro ha
IV	Småtjärn N. C 118	1,5	11,5	B	20	5	13	8,3
	Ulvsjön C 149	134	12	BQACE	450	150	300	2,2
	Vallsjön D 29	162	15	BHPQAF C	550	630	590	3,6
	Harsjön D 128	31	19	BH	200	19	110	3,5
	Sicksjön B 88	333	22	BHPQACE	2.200	850	1.525	4,6
	Öfsjön St., A 141	310	29	BHPQACEÄ	300	700	500	1,6
	Ansjön D 2	825	30	BHPQAFCE	2.100	1.300	1.700	2,1

¹ Bezeichnungen wie im Tab. 1.

mutlich der einzige Fall mit zuverlässigen Angaben, habe ich gefunden (ALM l.c.), dass der Hektarertrag zwischen 1,0 und 10,8 kg variiert mit einem Mittel von 5,4 kg. Alle diese Angaben zeigen somit einen niedrigeren Hektarertrag als die von den Kälarne-Seen erhaltenen.

Trotzdem diese letzteren Ziffern etwas hoch sein mögen, ist von Interesse zu sehen, wie der eben genannte von NORDQUIST gefundene Zusammenhang zwischen Hektarertrag, Grösse und Tiefe der Seen auch für die Kälarne-Seen zutrifft. Ein gewisser Zusammenhang ist schon aus Tabelle 18 ersichtlich. Dies gilt teilweise Seen innerhalb jeder Gruppe, verglichen untereinander von den geringeren zu den grösseren Tiefen, und teilweise Seen der Gruppe I und II verglichen mit denen der Gruppe III und noch mehr der Gruppe IV, innerhalb welcher die Anzahl der grösseren Seen zunimmt. Dieser Zusammenhang wird aber deutlicher, wenn die Seen innerhalb der bedeutenderen in Fig. 1 aufgezeigten Gewässergebiete miteinander verglichen werden. Es dreht sich dabei um Seen, innerhalb allgemein gesehen recht begrenzten Gebieten, mit etwa gleichen Fischarten, gleichartiger Fischerei und im allgemeinen mit Angaben von den gleichen Personen abgegeben. Eine diesbezügliche Aufstellung wurde in Tab. 19 gemacht, wo die Seen innerhalb der aufgenommenen Gewässergebieten nach der Grösse geordnet wurden. Abgesehen von gewissen Ausnahmen, ist hier der Zusammenhang zwischen abnehmendem Hektarertrag und zunehmender Grösse der Seen sehr auffallend. Im allgemeinen nimmt auch die Tiefe mit steigender Grösse der Seen zu. Die Abweichungen hierbei erklären die soeben genannten Ausnahmen. Für den Gewässergebiet *f* hat also der recht kleine Högtjärn einen niedrigeren Hektarertrag, vermutlich auf seiner grossen Tiefe von 12 m beruhend. Im Gewässergebiet *h* hat der grösste See der Hemsjön eine Tiefe von nur 9,5 m und sicher als Folge davon einen hohen Hektarertrag. Schwerer ist zu erklären, warum der im gleichen Gewässergebiet belegene, verhältnismässig kleine und sehr flache See Flarken verglichen mit den gleichartigen Seen Hongsjön und Skällsjön einen so niedrigeren Hektarertrag gibt. Auch der Singsjön im Gewässer-

Tabelle 19. Zusammenhang zwischen Grösse und Tiefe der Seen in gewissen Wassergebieten und ihre Hektar-Erträge.

Wasser- gebiet	Name	Grösse in ha	Tiefe in m	Hektar- Ertrag
f.	Loktjärn D 79	3,5	4	12,8
	Krångtjärn D 78	7	4	10,7
	Högtjärn D 36	8,5	12,5	1,9
	Gransjön D 8	50	8	5,5
	Balsjön D 7	64	7	7,8
	Bodsjön D 82	70	8	4,0
	Hällesjön D 37	125	16,5	3,4
g.	Lugnsjön D 119	350	14	2,3
	Öfström C 67	41	5	9,1
	Gastsjön C 66	140	9	3,3
	Mellansjön C 68	150	11,5	2,8
h.	Ansjön D 2	825	30	2,1
	Flarken A 152	31	2,5	6,1
	Hongsjön B 123	41	4,5	14,0
	Skällsjön B 117	56	3	10,5
	St. Öfsjön A 141	310	29	1,6
	Sicksjön B 88	330	22	4,6
i.	Hemsjön B 89	350	9,5	7,3
	St. Gäddtjärn B 121	1,5	4	12,7
	Nästjärn B 105	2	4,5	10,0
	Kvarnsjön B 104	10	3	6,3
	Lillsjön B 126	53	5	4,3
Fisksjön B 90	420	23	2,6	
Singsjön B 124	640	10	2,8	

gebiet *i* mit einer Tiefe von nur 10 m, müsste eine höhere Ziffer als nur 2,8 kg aufweisen können. Die Erklärung hierzu liegt vermutlich in der beträchtlichen Grösse des Sees. Weiter kann von den zwei Saiblingseen angeführt werden, dass der Hektarertrag in dem 17 m tiefen Storörmyrtjärn 3,7 kg, im Ö. Rörtjärn mit nur 7,5 m Tiefe dagegen 12,5 kg ausmacht.

Die recht grossen Abweichungen in Tab. 18 innerhalb der eben genannten Zusammenhänge beruhen meist auf den ausserordentlich variierenden Ziffern der vielen hier und dort belegenen, mehr isolierten Kleinseen. Abgesehen davon, ist aber doch der Zusammenhang offensichtlich. Die Ursache dazu ist, wie schon Nordquist betont hat (l.c.) und wie hier oben mit Vontjärn und Ilvästjärn als Beispiel besprochen wurde, dass die vom Gesichtspunkt der Produktion günstigere Litoralregion ein verhältnismässig grosses Areal in einem kleineren und dabei flacheren als in einem grösseren und dabei tieferen See einnimmt.

Der zurückgehende Hektarertrag der Seen von Gruppe I zu Gruppe IV hat darum sicher nichts mit den limnologischen Verschiedenheiten bei diesen Gruppen zu tun, sondern hängt damit zusammen, dass die Grösse und Tiefe der Seen im allgemeinen von Gruppe I bis Gruppe IV zunimmt.

Einen Zusammenhang zwischen Hektarertrag und den vorkommenden Fischarten (Fig. 29) gibt es kaum. Bei der Mehrzahl der Seen spielt Barsch

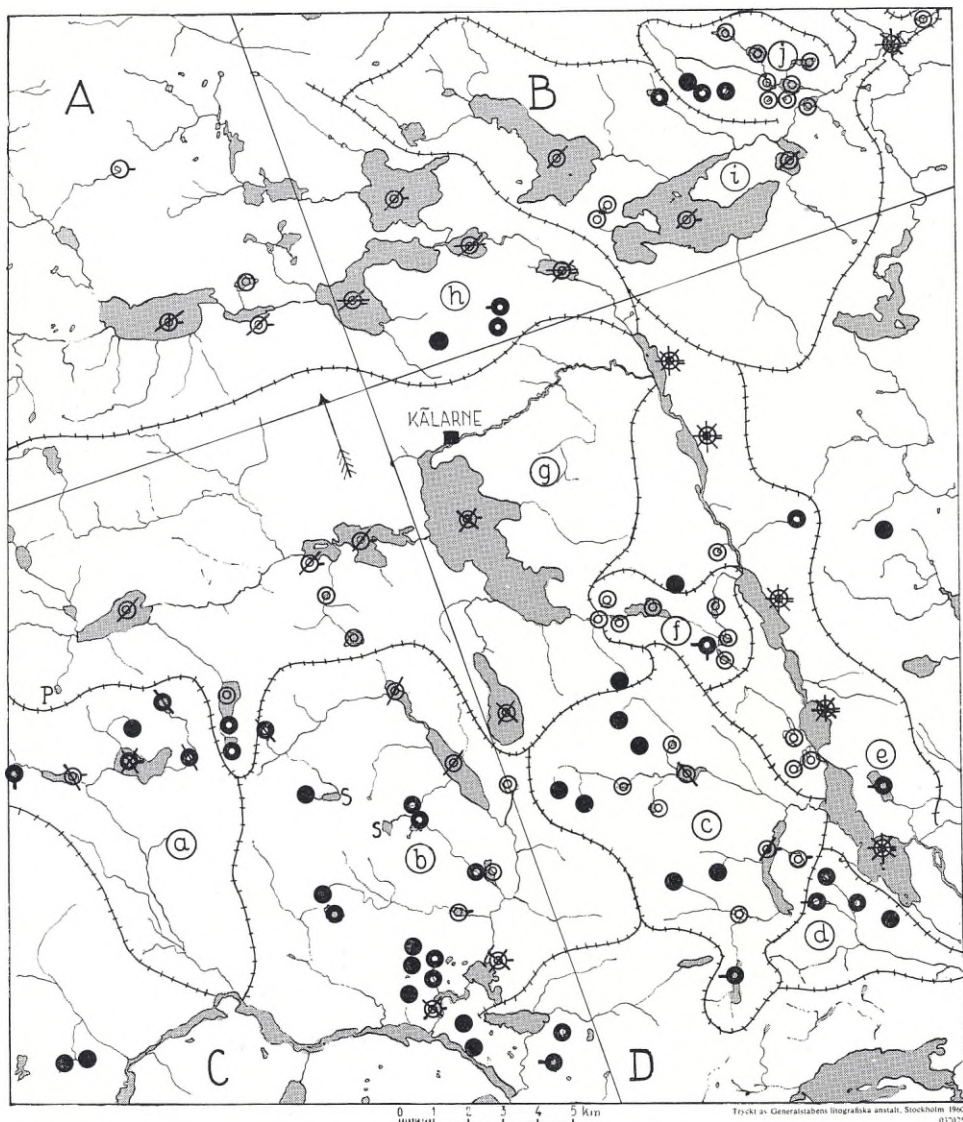


Fig. 29. Die in den Kälarne-Seen früher vorkommenden Fischarten.

● = fischleer; ○ = nur Barsch; ⊙ = Barsch, Hecht, Plötze, Quappe, Aal; ⊕ = Coregonen;
 ⊚ = Forelle; ⊖ = Brachsen; ⊕ = Äsche; -○ = Hecht; ○ = Elritze, Uckelei; S = Saibling.

Vergl. Fig. 1 und Tab. 18.

und Hecht die Hauptrolle. In verschiedenen der grösseren Seen kommen Coregonen, vereinzelt auch Forelle, Äsche und Brachsen hinzu. In Kleinseen mit nur Barsch ist der Hektarertrag manchmal sehr hoch, nämlich 10—12 kg, in anderen wieder sehr nieder, 1—2 kg. Dies hängt direkt mit der Individuengröße des Barsch zusammen, die in diesen Kleinseen sehr variiert.

VI. Die Bedeutung der fischleeren Seen für die Hausbedarf- und Sportfischerei

In der Einleitung wurde hervorgehoben, dass die Absicht mit den limnologischen Untersuchungen und Fischaussatzversuchen in den Kälarne-Seen in erster Linie war, die Möglichkeiten und die Bedeutung derselben und besonders der fischleeren Seen für den Fischfang zu ermitteln. Die Resultate haben nun gezeigt, dass in einer grossen Anzahl von solchen fischleeren Kleinseen mit Vorteil verschiedene Fischarten ausgesetzt und dadurch gute Fangmöglichkeiten geschaffen werden können. Auf der anderen Seite haben viele Aussätze keine positiven Resultate gegeben, wo nämlich die O₂-Verhältnisse der Seen zu schlecht waren, oder wo schon Barsch vorhanden war.

Es wurde weiter hervorgehoben, dass die Wiederfänge der geglückten Aussätze im allgemeinen keine besonders grossen Hektarerträge repräsentiert haben, auch wenn die Anzahl erhaltener Exemplare und das Gewicht derselben ziemlich hoch war. Doch wurde gleichzeitig darauf hingewiesen, dass mehrere andere Faktoren, vorwiegend Raubfang herein gewirkt haben. Bei einem Fischwasserbesitzer, der seine Wasser bewachen kann, können deshalb bedeutend höhere Erträge, als die bei diesen Versuchen erhaltenen, berechnet werden.

Es ist nun von Interesse, mit Hilfe der Ziffern in den Tabellen des III. Kapitels einige summarische Berechnungen über die Kosten der geglückten Aussätze anzustellen und diese Werte mit den Werten der wiedergefangenen Fische zu vergleichen. Die Kosten wurden zum Einkaufspreis des Aussatzmaterials berechnet. Der Preis betrug von jeweils 1.000 Exemplaren Kr 6 für Brut der Coregonen, Kr 30 für Brut der Salmoniden, Kr 300 für einjährige, Kr 800 für zweijährige solche. Die Kosten für Transporte und Arbeitszeit wurden nicht einberechnet. Der Wert der wiedergefangenen Fische wurde nach den landläufigen Marktpreisen berechnet, nämlich 2 Kr pr kg für Coregonen und 5—6 Kr per kg für Salmoniden.

Was die Aussätze von Salmoniden wie Forelle, Saibling, Bachsaibling und Kreuzungen betrifft, findet man, dass gewisse solche ein sehr gutes ekonomisches Resultat gegeben haben. So können die Kosten für die Aussätze bezw. der Wert der Wiederfänge berechnet werden für Forelle im Hundtjärn ca. 30 und 50 Kr, für Saibling im V. Rörtjärn ca. 160 und 300 Kr, für Saibling×Bachsaibling im Nissetjärn ca. 30 und 60 Kr. In anderen Fällen waren Kosten und Wert übereinstimmend, z.B. bei Forelle im Grästjärn und Stockbergstjärn, für Bachsaibling im Nissetjärn und Ö. Vontjärn. Bei mehreren Aussätzen waren aber die Kosten grösser als der Ertragswert. Die Anzahl der wiedergefangenen Fische ist doch in vielen dieser Fälle ziemlich gross gewesen, und in mehreren Seen wurden Gewichte der einzelnen Fische von 1—2 kg erreicht. Solche Fische sind ja vom Gesichtspunkt der Sportfischerei aus sehr begehrt. Diese Kleinseen können darum als Wasser für die Sportfischerei wesentlich

höhere Einnahmen erzielen. Die Mehrzahl dieser letzteren Aussätze kann aus diesem Grund als ökonomisch geglückt angesehen werden. Ein See, in dem ein Aussatz den reinen Betrag betreffend, günstig verlief, kann natürlich noch besser ausgenützt werden, wenn er der Sportfischerei zur Verfügung gestellt wird.

Es ist selbstverständlich, dass die Kosten für die Aussätze hätten bedeutend heruntergedrückt werden können, wenn Brut verwendet worden wäre an Stelle von in diesem Fall so oft angewandten einjährigen oder älteren Fischen. Mehrere Brutaussätze haben auch gute Resultate gegeben. Es ist doch sicherer mit älterem Aussatzmaterial.

Was die Aussätze von Coregonen und Coregonen-Kreuzungen betrifft, waren diese fast ohne Ausnahme ökonomisch lohnend und in mehreren Fällen besonders vorteilhaft. So z.B. im Ö. Vontjärn mit einem Kostenpreis von ca. 150 Kr und einem Ertragswert von ca. 220 Kr, im Svarttjärn C 279 mit resp. ca. 15 und 100 Kr, im Grästjärn mit ca. 20 und 90 Kr. Nur in wenigen Fällen hat sich der Ertragswert nicht mit den Aussatzkosten gedeckt.

Dass das Verhältnis zwischen Kosten und Ertragswert hier oft so vorteilhaft war, beruht teilweise darauf, dass das Aussatzmaterial von Coregonen beinahe immer Brut war, teilweise auf durchgehend grösseren Wiederfängen dieser Coregonen-Aussätze. Andererseits ist der Verkaufswert geringer, auch kann ein See mit nur Coregonen nicht für die Sportfischerei ausgenützt werden.

Wenn nun noch die Anzahl der ausgesetzten Brut beachtet wird, ist aus den Tabellen ersichtlich, dass diese oft sicher unnötig gross war und wahrscheinlich sogar manchmal eine verschlechterte Zuwachs mit sich brachte. Dies gilt z.B. dem späteren Aussatz einer Coregonen-Kreuzung im Grästjärn. Dieser gab allerdings einen Wiederfang von 320 Exemplaren aber mit einem Gewicht von nur 14 kg, gegen einen früheren Aussatz mit ebenfalls 300 Wiederfängen aber einem Gewicht von 58 kg. Ein Beispiel für eine niedere Brutmenge mit gutem Resultat ergab der 8 ha grosse Svarttjärn C 279, in dem nur 900 Brut ausgesetzt wurden mit 119 Wiederfängen von 53 kg. Sicher fällt der Aussatz von 100 oder einigen 100 Brut per ha sehr gut aus in diesen Seen.

Die Resultate, die bei diesen Aussatzversuchen erhalten wurden, sind selbstverständlich an und für sich nicht besonders bemerkenswert. Aber sie zeigen doch durch sichere Ziffern an, was man von solchen Kleinseen ohne teure Vorbehandlungen erwarten kann. Kleine fischlere Seen befinden sich in grösserer oder kleinerer Menge in privatem wie auch staatlichem Besitz. Wofern die Frage nach der Ausnützung dieser Seen aufgeworfen wird, muss doch betont werden, dass vollständig isolierte Wasser ohne O₂-bereichernde Zuflüsse bezw. Durchläufe und mit geringeren Tiefen als 2 u. 3 m gewöhnlich nicht geeignet sind, da man hier mit dem Eintreten totalen O₂-Mangels im Winter rechnen muss. Wie oben berührt wurde, können aber solche Seen unter gewissen Verhältnissen zur Aufzucht von Brut im ersten Sommer angewendet

werden. Kleine Seen mit sehr steilen Ufern und grösserer Tiefe als 8—10 m sind auch nicht besonders geeignet. Auf Grund des begrenzten Zugangs zu für den Fisch erreichbarer Nahrung, muss man hier mit einem niederen Ertrag rechnen. Was die übrigen fischleeren Seen betrifft, sind diese zum Aussatz von Fisch geeignet. Es ist aber wichtig, sich erst zu vergewissern, dass die Seen wirklich fischleer sind. Kommen Barsch und vielleicht noch andere Fischarten darin vor, müssen grössere Junge der neuen Fischart gewählt, oder sollte zu den modernen aber leider recht teuren Rotenon-Behandlungen gegriffen werden.

Wo ein Aussatz gute Resultate gegeben hat, muss man sich auch darüber im klaren sein, dass die Aussätze nach einigen Jahren erneuert werden müssen, was auch nötig werden kann nach langen und kalten Wintern mit nachfolgendem O₂-Mangel und dadurch eintretender Fischsterblichkeit.

VII. English summary

Introduction

The program for the activities of the Kälarne Fishery Research Station as laid up in the beginning of the 1930's contained, amongst others, experiments aimed at utilizing the numerous small lakes and tarns in the neighbourhood, many of which were empty of fish, for sport-fishing and for local consumption. Lakes of this type are very common in large parts of the forest areas in northern Sweden. Although often of rather insignificant size, they can offer considerable advantages to the people living near them, provided the supply of fish is good.

The first questions to be answered were the following: Why are so many of these lakes entirely without fish? Can the planting of fish in these lakes be expected to be economically successful and, if so, what species should be tried and what principles applied? Would the stunted perch populations in some of them be improved by decimation, or could they be brought to a better standard of growth and a higher economic yield by some other means? Would it be advisable to introduce new species of fish into small lakes of this type, where several other species are already found? The investigations and experiments of the last decades have been carried out along these lines. It has to be pointed out that at the time, when the experiments were started, the now common rotenone-methods for the extinction of worthless populations of fish were not yet known.

Some earlier publications (ALM 1946, 1952) deal in greater detail with the stunted perch populations and with the possibilities of ameliorating their growth. Last year (ALM 1960) a detailed account was given of the limnological conditions in 130 mainly small, but also in some slightly larger lakes in the neighbourhood of Kälarne. In this connection also the species of fish

in these lakes were mentioned and the reasons discussed, why many of these small lakes contain no fish. The present paper deals with the transplantings of fish carried out in these lakes, its results, and the reasons for its greater or smaller success.

Situation and nature of the lakes

The Kälarne Research Station is situated in the eastern part of the county of Jämtland at about 63° northern latitude. The area forms part of the coniferous region of Norrland, the rock-floor consisting mainly of granite with locally interspersed greenstone and moraines, sometimes rich in lime. The majority of the lakes is altogether surrounded by forest, their shores often consisting of quagmires and more seldom of hard soil. (See Pl. I—III.) Cultivated ground and sparse habitations are found only around the larger lakes.

All the lakes are of oligotrophic type, but their humic standard varies within wide limits. This finds its expression in the transparency and the colour of the lakes which accordingly have been classified into 4 groups. Group I contains lakes with transp. < 2.0, group II transp. 2.1—3.0, group III transp. 3.1—5.0, and group IV transp. > 5.0. Average values for the transparency, as determined with the white disk, and for pH, according to Czerny's pH-scale, are given. For a number of lakes also alkalinity ($\text{cm}^3\text{n}/10 \text{ HCl}$ in 100 cm^3) and conductivity ($K_{20} \cdot 10^6$) are recorded. Water samples for the determination of temperature and content of O_2 have been taken in all lakes in summer as well as generally also in winter, occasionally also in spring. Samples have often been taken from one and the same lake in different years.

Number of transplantings of fish and the species used in them

In 92 of these lakes planting of fish has taken place (Tables 1 and 2 and Fig. 1 and 2). Frequently several species have been introduced in the same lake, bringing the total number of plantings to 207. Among them trout occupies the foremost place with 68, or 33 per cent, of the plantings, followed by different forms of coregonids with 60 plantings or 29 per cent. Then come char, brooktrout, and hybrids between them with 17 per cent. About 50 per cent of all plantings have been effected with fry (Table 3). Otherwise fingerlings of different ages and also bigger joungs have been used.

The results

In order to obtain an idea of the results test fishings have been carried out every autumn, often already in the year of the planting. Unfortunately an intensive fishpoaching has often taken place in lakes, where good results had been obtained. This has made the results of the test fishings misleading.

Plantings with more than 15 recaptured fishes have been considered successful, and have been assigned 2-results. In the small lakes that are in question here the catching of, say, 16 often fairly large trout must be deemed a good result from the sporting point of view. Most often the number of recaptures has been far greater. Plantings with 6—15 recaptures have been designated as transitional or 1-results. No or at most 5 recaptures have been designated with 0. Fig. 2 shows the situation of lakes with different results.

Growth and size of fishes recaptured during different years in lakes with 2-results can be followed in Figs. 8—27. The Tables 4—12 contain also further information about these plantings, viz. year of planting, number and age of the material used, and also of the recaptures during the following years.

The results for the different species have been compiled in Table 13. There it can be seen that 54 plantings or 26 per cent have yielded 2-results, while 30 plantings or 14 per cent gave 1-results, the total thus being 40 per cent. Certain compilations of earlier plantings of fish in Sweden have given a total of about 27 per cent of good and moderate results for the years 1850—1916 (ALM 1920), and about 29 per cent for the years 1917—1935 (BRUNDIN 1937). Thus the results obtained at Kälarne have been better than those with earlier plantings in mostly larger lakes containing fish.

Most of the 2-results have been obtained with the planting of certain forms of coregonids, brooktrout, and hybrids between char and brooktrout. But also trout and char have given good results. Plantings with pike-perch and lake herring have been altogether unsuccessful. Some plantings were made with the less valuable roach, minnow, and crucian carp. These latter have all done well and also led to new populations. In the discussed lakes the other species have, however, not had good spawning grounds. The fishes have admittedly often been ripe for spawning with fully developed roe and milt, but no propagation has in general taken place. Only two plantings of brooktrout have led to new populations in the small outlet-brooks of the respective lakes, and propagation of whitefish may perhaps have taken place in one lake. (See Tab. 8 and Fig. 16.)

The causes of 0- and 1-results

The main causes of the negative results from the plantings at Kälarne are unfavourable O_2 -conditions and, in many lakes, the occurrence of perch. The Figs. 3 and 4 show the T- and O_2 -content in lakes in which these conditions are more or less unfavourable. In several of these lakes the O_2 -content of the hypolimnion was fairly low or zero already in summer. During the winter O_2 was in many cases altogether absent. On this account plantings have been unsuccessful in these and similar lakes. This was the case also with many plantings of fry and even of one summer-old fingerlings in lakes with perch.

In these cases the usually abundantly occurring small perch has been a serious competitor and a dangerous predator on the freshly planted fish. Also earlier planted fish which has done well could in many cases be compared with perch, and has prevented a favourable result of a later planting.

The 2-results

The good results have been obtained mainly in lakes empty of fish and with fairly good O₂-conditions. Figs. 5—7 show the T- and O₂-curves for several lakes of this type. In spite of the fact that the T- and O₂-curves often are strongly clinograde, the content of O₂ is nevertheless rather high in the epilimnion. In certain lakes, e.g. Vontjärn D 73 (Fig. 4) and Grästjärn D 69 (Fig. 4) it can nevertheless drop considerably in winter in certain years. The planting experiments have, however, shown that different forms of trout and coregonids and, in some lakes, also char and brooktrout do rather well in lakes in which the O₂-content did not exceed about 2 mg/l at times. It was just in the two above-mentioned lakes that several successful plantings of different species have been made. Their results are compiled in Tables 15 and 16. In similarity with other lakes, where 2-results have been obtained, these lakes have furthermore been of a decidedly dystrophic type with low transparency and brown water and mostly also with low values for pH, alkalinity, and conductivity as described earlier (ALM 1960). This proves that the salmonids and coregonids are not as particular about the environment as has often been assumed. Apart from the O₂-content which ought not to drop below 2 mg/l, the different results are probably due to competition with other species and the absence or presence of niches suitable for a freshly implanted species. To this have to be added the supply of food and its accessibility, when the size of the yield is taken into consideration.

The above-mentioned Tables 4—12 and Figs. 8—27 finally show that the number of recaptured fishes, especially among the coregonids, has often been very great. In some cases recaptures of more than 300 specimens of the planted fry have occurred. Table 14 gives the percentage of recaptured fishes for plantings with fingerlings and jounqs of different ages. This amounts in several cases to 50 per cent and more. Also the size of the recaptured fish has often been great, and in several of these small lakes a number of trout and char as well as coregonids weighing 1—2 kilogrammes have been caught.

The capture per hectare

Table 17 contains the calculated capture per hectare in lakes with 2-results, and in Table 18 similar informations are compiled about a number of lakes in the area of Kälarne that had previously contained fish, and which had been limnologically examined. It can be seen that the values in Table 17 are

fairly low. Provided that repeated plantings had been carried out and that the number of by poaching caught fishes could have been included the figures for the capture per hectare would have been much higher in many cases. It is, however, necessary to point out also in this connection that several lakes with the highest figures are of dystrophic type. This shows, apart from the above statement to the effect that salmonids and coregonids can do well in such lakes, that they can also give a fairly good yield. This is the case especially, if the litoral zone is comparatively extensive in comparison with the profundal zone. The former contains a richer fauna per surface unit. At the same time the O₂-conditions in the hypolimnion often become unfavourable in more steeply sloping and deeper small lakes of the types in question (ALM 1960). This can be exemplified by Ö. Vontjärn and Ilvåstjärn. These are very similar in many respects, but the morphometry (Fig. 28) and the T- and O₂-conditions (Fig. 4) are much more favourable for the fish in the former than in the latter lake. Growth and capture per hectare are also high in Vontjärn, but low in Ilvåstjärn.

If, however, all small lakes entered into Table 17 are taken into consideration, it is not possible to establish any closer connection between the productivity, expressed as capture per hectare, and the depth or size of the lake. The interrelation between the limnological conditions and the food accessible to the fish is probably more complicated in these small lakes than in larger lakes of a more harmoniously oligotrophic type. For larger Swedish lakes of varying types such a connection between yield, and size and depth of a lake has previously been established by NORDQVIST (1918). Also here the decisive feature lies in the relative extent of the litoral zone which is greater in a small lake than in a large one. Now Table 18 shows that such a connection exists also in the somewhat larger lakes at Kälarne. This is particularly evident, if lakes within a certain drainage system (see Fig. 1) are compared with each other. This has been done in Table 19. There the lakes of each drainage system are entered in order of growing size, and the capture per hectare increases on the whole in the same direction. The exceptions from this rule depend mainly upon the depth. For this reason a small but deep lake can have a yield which is lower, and a large but shallow lake one that is higher per hectare than might be expected from the comparison of its size with that of other similar lakes within the same area.

The value of lakes empty of fish from the point of view of fishery

The numerous successful results of the planting experiments that have been carried out have shown the following. Many small lakes empty of fish can be suitably planted with different forms of salmonids and coregonids, sometimes also with char and brooktrout. Often the value of the recaptured fish already more than repays the expense of the planting. Yet much greater

revenues can be realized, if these small lakes are made accessible to sport-fishing. One has, however, to be prepared for the necessity of renewed plantings, either on account of the fact that propagation fails to take place or that the fish die by suffocation, when during long winters with plenty of snow the O₂-conditions become too unfavourable. Also in small lakes with only perch the planting of the above-mentioned species may turn out well, but ought to be effected there with larger fingerlings reared in ponds or with young of trout and brooktrout transferred from other lakes. If, however, perch or other less valuable fish are very common and small-sized, it is safer to use the now common rotenone methods and entirely eliminate the original population.

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Nachschrift

Übersicht der Resultate einiger Probefänge im Herbst 1961.

Vergl.	Fischart	See	Alter	Sämtl.	Gewicht in kg	Länge in cm
Tab. 9 S 43	„Smerling“ × „storsik“	Grästjärn D 69	7	42	4,0	21—30
„ 9 „ 43	„ „ „	Långsmaltjärn C 49	7	33	0,9	16—20
„ 10 „ 49	Kl.Mar. × „storsik“	Ö. Vontjärn D 73	5	65	28,1	31—39
„ 10 „ 49	„ „ „	Ö. Gravtjärn C 198	9	57	12,4	25—32
„ 10 „ 49	„ „ „	Dracksjön C 266	5	4	0,6	21—31

Zooplankton and impoundment of two lakes in Northern Sweden (Ransaren and Kultsjön)

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Introduction

In the summer of 1954, the Institute of Limnology in Uppsala started an investigation of two lakes, Ransaren and Kultsjön in Northern Sweden. That year the building of a power dam had been started at Ransaren and the Institute was requested to investigate the limnological conditions of the lake with special respect to the future changes, which might be due to the regulation. Kultsjön was, at that time, untouched and the samples taken in it were to be used as a reference material.

The research work was led by Professor Wilhelm Rodhe in a team work together with other members of the staff. I did not myself join the team until the summer of 1956 from which time I have participated in the field-work and examined the zooplankton samples, including those taken in 1954 and 1955 which had not been worked up earlier.

Simultaneously with the limnological investigations, the Institute of Fresh-water Research, Drottningholm, carried out work on the bottom fauna and the fishes. The intention is, that all the results together will be of good use

in determining what happens to the fish populations, when a lake is regulated. The dominant fish species are the char *Salvelinus alpinus* and the trout *Salmo trutta*. They are of the greatest economical importance not least through the compensation claims which follow a decrease in the fishing, due to a regulation.

This paper deals only with the zooplankton. The primary production, phytoplankton, and the chemistry of the lakes are only discussed to the extent that is necessary to characterize the lakes or in connection with some special zooplankton problems. See further the papers by RODHE, KARLGREN, LINDGREN, NAUWERCK and RAGNBERG (in preparation).

The samples 1954—1956 have been taken every fortnight from the break-up of the ice at the beginning of June until the end of August. During the cold season there have, if possible, been three sampling periods, one in January, one in late spring and one in late autumn. In 1957 and 1958 I have increased the number of zooplankton samples in Ransaren in order to follow closer the seasonal variation of the species. In 1959 the main attention was paid to the conditions in the littoral zone. The regular sampling series were then reduced to the same intensity as in the beginning of the investigation.

Above and in the following the names of the lakes according to Swedish terminology have been used (Ransaren instead of Lake Ransaren and Kultsjön instead of Lake Kultsjön).

I. General characteristics of the lakes

Ransaren and Kultsjön are situated in the Swedish part of the Caledonian mountain range at about 65° North and 15° East. Ransaren has a length of about 14 km and an area of 21 km² at mean water level. It is situated 580 m above sea level. The corresponding values for Kultsjön are 30 km, 53 km² and 540 m. They can both be classified as oligotrophic lakes. As the trophical conditions of an unpolluted lake are solely depending on the morphology, edaphy, and climate of the surroundings, it is necessary to touch upon these factors in a few words.

At the end of the ice age these lakes made up part of an area of ice-dammed lakes, which were tapped at the last melting of the ice. Only the deeper basins remained as lakes, drained by rivers to the Bothnian Gulf. The levels of the lakes gradually sank due to the erosion of the rivers until they finally reached their present level. As to its shape, Ransaren is presumably not particularly interesting. It has a smooth shore-line and the bottom profile does not show any greater irregularities. The maximum depth is about 60 m. Kultsjön, on the other hand, is divided into at least three different basins (fig. 1). The east one has a most irregular shoreline. There are

a great many small islands and the bottom profile includes both the shallowest and the deepest parts of the whole lake. The maximum depth is about 140 m. This divergence between the two lakes has its probable explanation in the fact that the last ice-rest occupied the eastern part of Kultsjön and that the ice-shed in the final melting phase was lying in this area. As a result of this the above mentioned islands were formed. They are either terminal moraines or eskers with a morain cap. The eskers were formed by glacial rivers flowing both in an easterly and westerly direction because of the different position of the ice-shed. The northern basin up to Fatmomakke and the western basin between Stornäs and Klimpfjäll are more similar to Ransaren in shape.

The sampling station (fig. 1) include one main station in each lake, station 1, where samples have been taken every fortnight during the summer months, June—August, in 1957 and in 1958 also in September. At this station also the autumn, winter and spring samples were taken. The morphological agreement between Ransaren and the western basin of Kultsjön provides a good basis for a comparison between the two lakes and for this reason station 1 in this lake was chosen in western Kultsjön.

In the northern end of Ransaren (station 2 and 3) and in the eastern basin of Kultsjön (station 2 and (2)) samples have also been taken at regular intervals. These stations have served as a comparison between opposite parts of the lakes. The position of station 2 in Kultsjön has varied during the different years of investigation. Concerning the extra stations for zooplankton profiles in Ransaren the reader is referred to fig. 23 (page 126).

The geological structure around the lakes is of quite a simple character. The dominating rocks are seve- and köli-schists in varying degrees of transformation. Thus the rocks around Ransaren are mainly phyllites, while the surroundings of Kultsjön consist of mica-schists (RUDBERG 1954).

The soil around the lakes can be classified as sediments from the ice-lakes and the glacial rivers, and to some extent as moraines. There is no addition of fertilizers to the soil, because of the inconsiderable agriculture. The only form of manuring comes from the faeces of the reindeer, which, as a matter of fact, might play an important rôle at Fabmeluokte in the northern end of Ransaren, where for centuries the Lapps have had one of their meeting-places for the annual separation and marking of the reindeer and where there is also a good pasture for the animals.

The climate is of the cold temperate type according to Köppen. This climate zone is, however, very extensive and there is a big difference between the relatively warm southern part of Sweden and the northern mountain region with its cold winters and short summers. The mean temperature for January is about -10° and for July about $+12^{\circ}$ C. The lakes are covered with ice from the middle of November until the beginning of June. In summer the temperature is high enough for the development of a thermal strati-

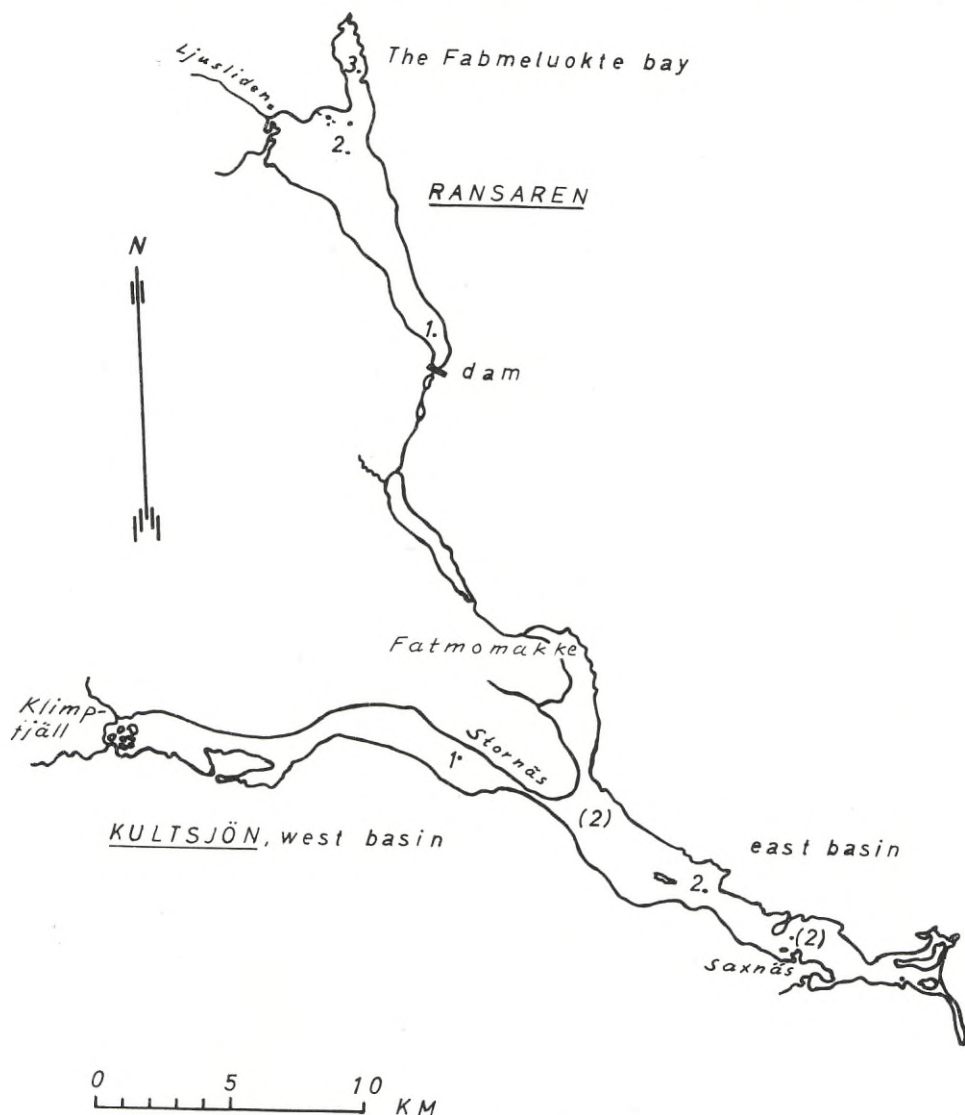


Fig. 1. Ransaren and Kultsjön with the sampling stations.

fication. This is, however, very unstable and may, quite easily, be broken down during longer periods of strong winds and cool weather. The precipitation is rather high, about 1200 mm per year, most of it falling in winter as snow.

In midsummer time there is a day-length of about 20 hours and the light available for the phytoplankton is abundant. In midwinter, on the other hand, the light intensity is very low and insufficient for phytoplankton production. Yet, the zooplankton is not specially poor during the same time and

the animals are dependent on a reproducing crop of phytoplankton. RODHE (1955) has given a probable explanation of this. He points out the possibility that the nannoplankton is not entirely restricted to an autotrophic mode of life, but under certain conditions some algae can also use dissolved organic matter as food. Thus the food uptake could alternate between autotrophy and heterotrophy.

The transparency, measured with a Secchi disk, is relatively high. The mean value varies between 8—10 m, but can decrease during the spring flood to 4 m in Ransaren.

As mentioned above the lakes are thermally stratified in summer. The temperature measurements in Ransaren in the summer of 1958 (Ragnberg personal communication) give a good picture of the thermal conditions.

After the unusually late break-up of the ice that year the water temperature slowly rose until the end of June, when there was a sudden rise caused by unusually hot weather. The air temperature amounted to more than 25°C during daytime. This warm period lasted for about one week and created quite a remarkable temperature distribution in the lake. During that period a weak southern wind brought the warm surface water to the northern end of the lake. The temperature at station 1 was 4.5° almost from the top to the bottom, while at station 2 the surface water had a temperature of 12.4° (see fig. 7). This displacement caused an irregular distribution of the plankton, which will be dealt with in a later chapter. The warming of the water continued for a couple of days, and the uppermost layers reached a temperature of $16\text{--}17^{\circ}$. On the 3rd of July the wind shifted to north-west and the air temperature began to fall. This cold weather lasted to the 19th when the wind veered to south-east and the air grew slightly warmer. The air temperature was, however, still low and remained so another couple of days. A temperature profile in the lake on the 24th revealed that the stratification was practically broken down and that the difference between surface and bottom was only 0.9° . The lake was at that time almost in circulation. Warm weather during the later part of August raised the temperature of epilimnion to above 10° . During the last days of August a period of very warm days set in, but the back-radiation during the relatively cold nights prevented any effective warming of the water. In the middle of September, when the summer investigation was completed, the lake was almost homothermal at station 1 with a water temperature as high as 11° between 1—10 m. These conditions were caused by very strong winds.

The above described temperature course in Ransaren provides an excellent example on the very unstable conditions in lakes of this type.

The reverse stratification in winter shows a temperature gradient of about $2\text{--}2.5^{\circ}$ between surface and bottom water. The bottom temperature never amounts to $+4^{\circ}$, because of the strong cooling in late autumn, when the air

Table 1. w. = winter, sp. = spring, s. = summer, a. = autumn. The spring, winter, and autumn values represent the variation within one vertical series, while the summer values represent the whole summer. Extreme values are excluded.

	1957				1958				1959	
	w.	sp.	s.	a.	w.	sp.	s.	a.	sp.	s.
Ransaren										
pH	7.4-7.6	7.2	6.4-7.3	7.2	7.0-7.5	7.1	6.8-7.2	7.2-7.3	7.1	7.1-7.4
Alk. m.equiv/l	0.27-0.33	0.31-0.32	0.24-0.29	0.28-0.29	0.28-0.40	0.30-0.31	0.24-0.32	0.28-0.29	0.28	0.26-0.28
O ₂ mg/l	11.6-13.3	11.7-11.9	7.5-11.7	10.9-11.1	10-14.2	10.4-11.5	9.4-11.1	10.3-10.7	11.7-11.9	9.3-12.7
z · 10 ⁶	40-46	43	33-42	40	41-52	39-41	33-40	37-38	41	37-40
PO ₄ -P γ/l	0.0-0.2	0.0-0.9	0.0-1.3	0.2-0.9	0.2-2.9	0.8-4.1	0-2.4	0.9-1.3	1.0-1.4	0-1.0
NO ₃ -N γ/l	20-41	0-1	0-32	9-19	27-57	25-35	10-39	29-45	14-38	2-48
Kultsjön										
pH	7.2-7.6	7.0-7.1	6.5-7.2	6.7-6.8	6.8-7.2	7.0-7.1	6.7-7.3	7.1-7.3	7.0-7.2	6.8-7.4
Alk. m.equiv/l	0.18-0.29	0.25	0.19-0.23	0.22-0.23	0.21-0.35	0.25-0.26	0.15-0.24	0.22-0.23	0.22-0.23	0.20-0.22
O ₂ mg/l	11.3-12.5	11.5-12.6	9.2-11.7	11.3-11.5	11.4-15.6	11.5-11.8	9.4-11.4	10.9-11.1	11.9-12.1	9.7-12.8
z · 10 ⁶	34-42	35-36	27-35	33-34	32-46	34	24-33	31-32	33-36	31-36
PO ₄ -P γ/l	0.0-0.5	0.0-0.6	0.0-1.0	0.0-0.7	0.0-0.6	0.7-1.6	0.0-0.8	0.0-0.5	0.5-0.6	0.2-4.1
NO ₃ -N γ/l	27-36	7-24	0-18	0-25	28-51	28-30	0-34	26-52	35-41	12-41

temperature is several degrees below zero and the winds prevent the lakes from freezing.

The chemical analyses of the water samples clearly illustrate the oligotrophic character of the lakes. Because of the fact that the chemical conditions will be treated thoroughly in a special paper by Lindgren it is quite sufficient to present a summarizing table with chemical data, which have kindly been left at my disposal (Tab. 1).

The phytoplankton (NAUWERCK 1957) is dominated by the more or less colourless Chrysoomonads *Monochrysis*, *Chromulina*, and *Monas* and the diatoms *Asterionella formosa* and *Cyclotella Kuetzingiana*. The total volume varies between $5 \cdot 10^6 \mu^3/l$ and $500 \cdot 10^6 \mu^3/l$ with a mean value for the photosynthetic layer of about $120 \cdot 10^6 \mu^3/l$.

II. Methods

Both quantitative and qualitative samples have been taken. The apparatus used for the quantitative collecting was a plankton sampler described by RODHE (1941). It is a 5 litre sampler, which by means of a messenger is brought to close at a desirable depth. The water is then passed through a gauze wire with a mesh-size of about 70 μ . Such a filter retains most of the planktic animals except the protozoans. Of course there may be a loss even of small rotifers when they occasionally pass the filters in a perpendicular direction. As a matter of fact the best quantitative results are to be expected when the water is moderately rich in bigger phytoplankters and the filter is to some extent clogged. Following PEJLER (1957) I have tried to use double filters to prevent losses, but unfortunately this is not always applicable as the clogging of the filters causes too long sampling times. After filtering the water the animals obtained have been preserved in 4 % formaldehyde and counted by means of a reversed microscope.

The results are presented in tables and diagrams. The greatest difficulty when drawing the diagrams has been to find an adequate way to express the density of the standing crop of zooplankton. As it is not possible to take samples from every meter in a 40 m deep lake, every interpolation between the reduced number of samples will inevitably be a little hazardous. Yet this is the only way to work, and I have chosen to base the diagrams of the seasonal variation on calculations of the number of individuals per dm^2 . The diagrams that show the vertical distribution have been drawn in a linear scale and thus diverge from the usual way to reproduce the distribution, namely by means of the third root of the values.

The depth at station 1 and 2 in both the lakes has not permanently been 40 m, but for practical reasons this depth has always been used when constructing the different diagrams. I find it quite justifiable to do so when

dealing with the same stations all the time and the depth varies within moderate limits. When comparing the quantitative values for different years and stations it would be too uncertain to use the exact depth as a change of only a few meters may increase or decrease the number of individuals calculated per surface unit even when there is no change in the population densities.

Some diagrams are based on the zooplankton volumes. The calculation methods and the volumes of some species are given in chapter VII and the reader is therefore referred to this chapter for further information.

III. The composition of the zooplankton

The purpose of this investigation was to study the zooplankton as a whole. The collected samples are numerous and make up a good material for careful studies of the biology of the species. In this case, however, it is for many reasons desirable that the publication of the results will not be too late. Therefore only a few species have been thoroughly studied and even in these cases much more remains to be done, including laboratory experiments, which I unfortunately have not been able to do. The results presented in this chapter are mainly from Ransaren in 1958, when the investigation was most intensive.

Table 2. List of the species (R=Ransaren, K=Kultsjön).

A b u n d a n t:	<i>C o p e p o d a</i>
	<i>Cyclops scutifer</i> SARS (R, K)
	<i>C l a d o c e r a</i>
	<i>Bosmina obtusirostris</i> LILLJEBORG (littoral zone, R)
	<i>Polyphemus pediculus</i> LINNÉ (littoral zone R, K)
	<i>R o t a t o r i a</i>
	<i>Polyarthra vulgaris</i> CARLIN (R, K)
	<i>Kellicottia longispina</i> KELLICOTT (R, K)
	<i>Keratella cochlearis</i> GOSSE (R, K)
	<i>Conochilus unicornis</i> ROUSSELET (R, K)
C o m m o n:	<i>C o p e p o d a</i>
	<i>Diaptomus laticeps</i> SARS (R)
	<i>Diaptomus graciloides</i> LILLJEBORG (K)
	<i>C l a d o c e r a</i>
	<i>Daphnia galeata</i> SARS (R, K)
	<i>Bosmina obtusirostris</i> LILLJEBORG (pelagical zone R, K)
	<i>Holopedium gibberum</i> ZADD (R, K)
	<i>R o t a t o r i a</i>
	<i>Synchaeta truncata</i> VON HOFSTEN (R, K)
	<i>Synchaeta pectinata</i> EHRENBERG (R, K)
	<i>Polyarthra dolichoptera</i> IDELSON (R, K)
	<i>Asplanchna priodonta</i> GOSSE (R, K)
<i>Filinia terminalis</i> PLATE (R, K)	
<i>Collotheca mutabilis</i> HUDSON (R, K)	

Table 2. Cont.

Less common:	<i>Copepoda</i>
	<i>Heterocope saliens</i> LILLJEBORG (R, K)
	<i>Cladocera</i>
	<i>Polyphemus pediculus</i> LINNÉ (pelagical zone R, K)
	<i>Sida crystallina</i> O. F. MÜLLER (R)
	<i>Daphnia hyalina</i> LEYDIG (littoral zone R)
	<i>Rotatoria</i>
	<i>Argonotholca foliacea</i> EHRENBERG (R, K)
	<i>Keratella hiemalis</i> CARLIN (R, K)
	<i>Ploesoma hudsoni</i> IMHOF (K)
	<i>Ascomorpha saltans</i> BARTSCH (R, K)
Rare:	<i>Copepoda</i>
	<i>Diaptomus laticeps</i> SARS (K)
	<i>Cladocera</i>
	<i>Chydorus sphaericus</i> O. F. MÜLLER (R, K)
	<i>Rotatoria</i>
	<i>Notholca labis</i> GOSSE
	<i>Trichocerca cylindrica</i> IMHOF
	<i>Euclanis dilatata</i> EHRENBERG
	<i>Euclanis parva</i> ROUSSELET
	<i>Lecane</i> spp.
	<i>Trichotria porcillum</i> VOIGT
	<i>Mytilina mucronata</i> O. F. MÜLLER
	<i>Monommata</i> sp.
<i>Distyla</i> sp.	

Most of the rare rotifers are found in Ransaren. This, however, does not mean that they do not occur in Kultsjön, but only that Kultsjön is not investigated to the same extent.

Copepoda

Cyclops scutifer. This species is very common in Ransaren and Kultsjön. The course of development is the same in both the lakes. Because of the interesting phenomenon of a dualism within this species it has been quite thoroughly studied, and I have therefore preferred to deal with *Cyclops scutifer* in a special paper (AXELSON, 1961), to which the reader is referred to obtain the results of my investigation.

Diaptomus laticeps. This species is common in Ransaren in summer, while only a few individuals have been found in Kultsjön, probably brought there by the inflow. The annual variation of *D. laticeps* is pronouncedly monocyclic.

In the samples from late winter *D. laticeps* is only represented by nauplii. In May when there is still an ice-cover on the lake the development of copepodites has began. These pass their growth stages mainly during June. At the end of June the first adults are found, and the number of adults increases during July to reach a peak in the beginning of August. Then the population

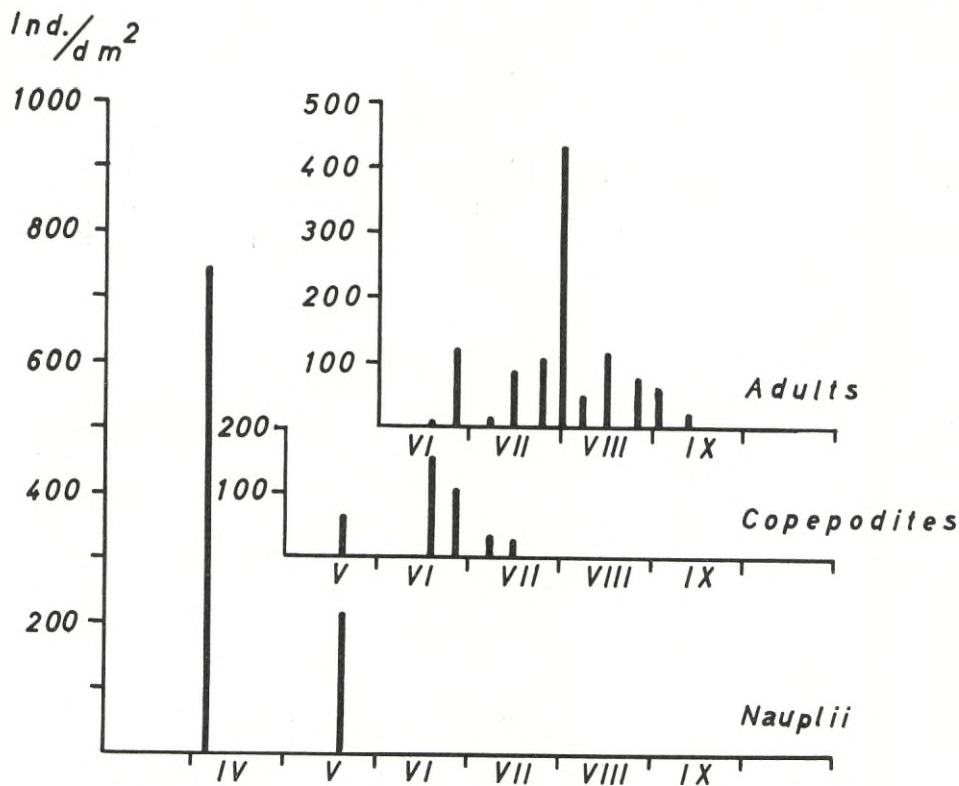


Fig. 2. The development of *Diaptomus laticeps* in Ransaren in 1958.

declines, but still in September both egg-carrying females and males can be found. The eggs are resting eggs, which next spring will develop into nauplii.

Because of lack of samples during the time for the development into copepodites it has not been possible to investigate the different copepodite stages in *D. laticeps*. GURNEY (1929) has described a dimorphism in the adult stages and LINDSTRÖM (1958) reports a dualism similar to that of *Cyclops scutifer*. The first author has found values for the size variation in the adults, which for the smallest individuals vary between 1.12—1.43 mm in the females and reach a value of 1.17 mm in the males. The corresponding values for the bigger animals are 1.26—1.60 mm in the females and 1.30 mm in the males. In Ransaren the majority of the males reach a length of about 1.4 mm and the females up to 1.75 mm.

Diaptomus graciloides. Like *D. laticeps*, which represents the genus in Ransaren *D. graciloides* is very common in the samples from Kultsjön. The annual cycle is presented in fig. 3.

There appears to be only one generation during the year. In the beginning of the summer (June) nauplii and adults are found. The former develop into

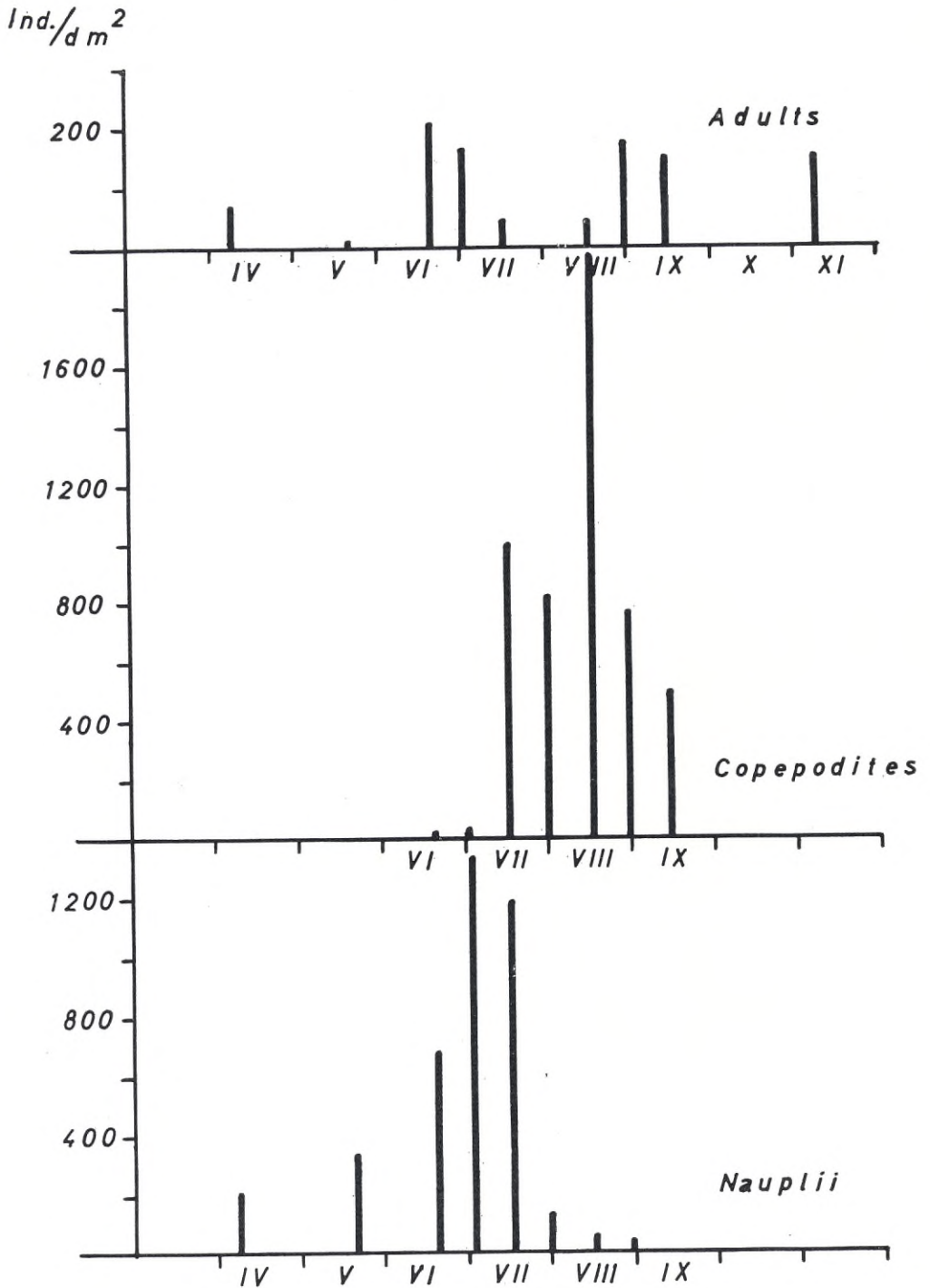


Fig. 3. The development of *Diaptomus graciloides* in Ransaren in 1958.

Table 3. Size variations in *Diaptomus graciloides*. Measures in μ .

	♂♂	♀♀
Cop. stage I	520—540	
" " II	610—660	
" " III	700—750	
" " IV	800—820	850—870
" " V	910—930	960—1,000

copepodites, which have their maximum in the late part of July and in August. The adults begin to appear in the middle of August and in September the population is still developing from old copepodites to adults. As to the hibernation of *D. graciloides* I am not sure. In the samples from late autumn only adult individuals are found. They are never seen carrying eggs and are probably not sexually mature. There is a possibility that the winter is passed by these males and females and that they do not become fertile until spring or early summer in the following year. The animals do not reach maturity at the same time. Some of them become fertile as early as in the beginning of April, while others do not produce eggs until in June. It is, however, my opinion that they all belong to the same generation. Unfortunately I have only two January series, namely from 1955 and 1957 but in these as well as in the samples from April 1958 and in every May series the adults are very few compared with the individuals from early summer. I therefore conclude that all the adults do not pass the winter in the free water, but most of them hibernate in the bottom mud or in the water close to the bottom, a case that is not rare in the copepods.

EKMAN (1904) has found at least two generations of *D. graciloides* in the larger lakes of northern Sweden. RYLOV (1935) states that this species can be either mono- or dicyclic and that resting eggs can be found. The findings in Kultsjön seem to contradict EKMAN in the sense that the annual cycle is most probably made up of only one generation, the course of which is the one described above.

Measurements have been made of the body length and from these results the following can be concluded. The different copepodite stages overlap each other in respect to body length, the limits are quite diffuse. Nevertheless the size variation in stage I—V shows the following values.

The table above shows that the size of all the animals seems to be the same in the first three copepodite stages, while in stages IV and V the females are bigger than the males. The mean length of the adult male and female is about 0.95 resp. 1.1 mm.

In an earlier paper (AXELSON 1957) I have touched upon the phenomenon of two different species of *Diaptomus* in two neighbouring lakes within the same water system. According to EKMAN (1904) *D. graciloides* is an immigrant

from the south following the border of the regressing ice. *D. laticeps*, on the other hand, is supposed to have immigrated from the east (RYLOV 1935 and THIENEMANN 1950). If this is correct, it remains to explain why *D. graciloides*, which most probably was the first settler in the area, did not also find Ransaren suitable for its demands. Or is there a possibility that *D. graciloides* in post-glacial time has inhabited also Ransaren, but could not compete with *D. laticeps*. The competition between different *Diatomus* species is quite well established and it is very seldom one can find representatives of two species in the same lake. Yet, as a matter of fact, *D. laticeps* is found in Kultsjön and what is more interesting, the findings are more frequent in the later years of the investigations. Now it is necessary to keep in mind that the material is too small to allow any definite conclusions, but I will propose a possible way in which the regulation of Ransaren may effect the spread of *D. laticeps* into Kultsjön.

No copepod can survive the swift water transport between the two lakes but as eggs. As *D. laticeps* reproduces by resting eggs, there is a possibility that they might be brought to Kultsjön by the inflow. The eggs, however, are lying on the bottom mud during the winter, and there is a very little chance for them to be carried out from Ransaren by the insignificant water-flow from the lakes in winter under normal conditions. In Ransaren, however, the discharge of the water after the regulation is mainly during January and February, and this big water-flow together with a disturbance of the bottom sediments down to a depth of 18 m, might bring about a transport of eggs from Ransaren, which is not possible under normal conditions.

Heterocope saliens. This big copepod has been found in small numbers in both lakes. The annual cycle is restricted to a proportionately short period in summer and the development from nauplii to adults is much faster than in the other copepods of the lakes. The nauplii appear from the end of June to the beginning of July. The copepodite stages are rapidly passed and in the beginning of August the first adults are found. They still remain in the samples from September. The reproduction is by resting-eggs which hibernate and do not hatch until the following summer. Concerning Ransaren *H. saliens* is not truly a pelagic form. In 1958 big swarms appeared in the littoral zone and I consider the species to be mainly littoral in this lake.

Cladocera

Daphnia galeata. Like *Cyclops scutifer* this common species has also been more thoroughly studied than the other zooplankton species and is dealt with in the same paper as *C. scutifer* (AXELSON, 1961). In the paper the reader will find data of the annual cycle and a description of the cyclo-morphosis as well as an attempt to connect the phenomenon of cyclo-morphosis with different environmental factors.

Daphnia hyalina. This species is entirely restricted to the littoral zone. Only a few individuals have been found in the ordinary samples. As the investigations of the littoral zooplankton are restricted to some series during a short period of the summers of 1958 and 1959 the seasonal course of this species has not been followed. All I can say is that *D. hyalina* is quite few in numbers in Ransaren and that the species might suffer from competition with *Bosmina obtusirostris*, which appears in great numbers in the littoral zone. Whether *D. hyalina* also is present in Kultsjön can not be said because no littoral samples have been taken in this lake.

Bosmina obtusirostris. Synonymous names are *B. coregoni obtusirostris* or in many papers only *B. coregoni*. The species in Ransaren and Kultsjön does not show any cyclomorphosis and according to EKMAN (1904) I have chosen the name *B. obtusirostris*. It occupies both the littoral and the pelagical zone but is much more abundant in the former. The maximum values found are higher than for any other zooplankton species in the lakes including the rotifers, namely 336 ind./l.

The number of individuals found in the pelagical zone varies greatly from year to year. I therefore conclude that *B. obtusirostris* prefers the near-shore water, especially the bottom water, and when the conditions are favourable in the littoral zone there is a spread out into the open water, where proportionately many individuals can be found, while under worse conditions only a few specimens are found far from the shore.

No sexual period has been observed during the ice-free season. A few males have been found in autumn and one single male in June in Kultsjön. The reproduction during the whole summer is thus by subitan-eggs and it is not settled how the winter is passed. It is possible that the sexual period does not coincide with the sampling periods in autumn, but still more probable is the possibility that the annual cycle is entirely acyclic and that the population hibernates with a sparse number of parthenogenetic animals in the littoral zone, where no samples have been taken during winter.

Other *Cladocera*. The species described above dominate the Cladoceran contribution to the zooplankton in the pelagical zone and *B. obtusirostris* as well in the littoral zone. Besides these some other species are frequently found in both the lakes. In the littoral zone *Polyphemus pediculus* occasionally appears in great numbers as was the case in 1958. In the open water only a few individuals are found at the ordinary stations. *Holopedium gibberum* is regularly found in the ordinary samples in varying numbers. A few males have been found but the population is too small to allow any conclusions concerning the reproductive periods. In the littoral net-plankton *Sida crystallina* has sometimes been found in Ransaren. A few specimens of *Chydorus sphaericus* have also been seen.

NILSSON (personal communication) has examined a great number of char stomachs from Ransaren. The investigation has shown that the cladoceran

Eurycerus lamellatus makes up an important food for the fish. However, this species has never been observed in the zooplankton samples, which may be due to its benthic manner of living.

Rotatoria

Though the rotifers from the volumetric point of view make up a very few per cent of the zooplankton they are in number and in richness of species a very dominating part of the plankton samples. As in the *Copepoda* and the *Cladocera* my description does not follow any taxonomic order but is arranged from the most abundant to the very sparse ones.

Polyarthra vulgaris and *Kellicottia longispina*. These two species are very common rotifers in both the lakes, in Ransaren sometimes reaching a number of more than 100 ind./l in the surface water. The annual cycles are very similar, at least in summer, and they are therefore dealt with together. When counting the quantitative samples I have not separated the two species *P. vulgaris* and *dolichoptera*, but as the former species makes up the main part of the genus *Polyarthra* in both the lakes, I find it justifiable to use the observed values for a calculation of the abundance of *P. vulgaris*.

In fig 4 the variation in the standing crop of *P. vulgaris* and *K. longispina* has been drawn. The values refer to station 1 and 2 in Ransaren in 1958. One can easily see the very good agreement between the two species.

There are two maxima in summer with an interval of about 30—40 days. It is noticeable that the time for maximum and minimum appearance at station 1 does not coincide with those at station 2, as well as the fact that the intervals between these periods are not of the same length. Leaving it an open question whether there is any real difference between station 1 and 2 in favouring zooplankton production, it might be stated that these irregularities most probably depend on a direct or indirect effect of the horizontal transport of the surface waters. The horizontal distribution of the zooplankton will be dealt with at length in the next chapter, and it will be enough here to say that the differences between station 1 and 2 do not only depend on a direct transport of the animals but under certain weather conditions long lasting displacement of warm surface water may arise, causing different conditions in one end of the lake than in the other.

Both the species are found throughout the winter, *K. longispina* in relatively great numbers (25 ind./l in some water layers), while *P. vulgaris* is quite rare and is succeeded by *P. dolichoptera*.

At the time for maximum development of *K. longispina* reproducing periods with resting eggs have been observed.

Keratella cochlearis. Common in both lakes during every season. There are at least two summer maxima (fig. 5 and 8), one at the end of July

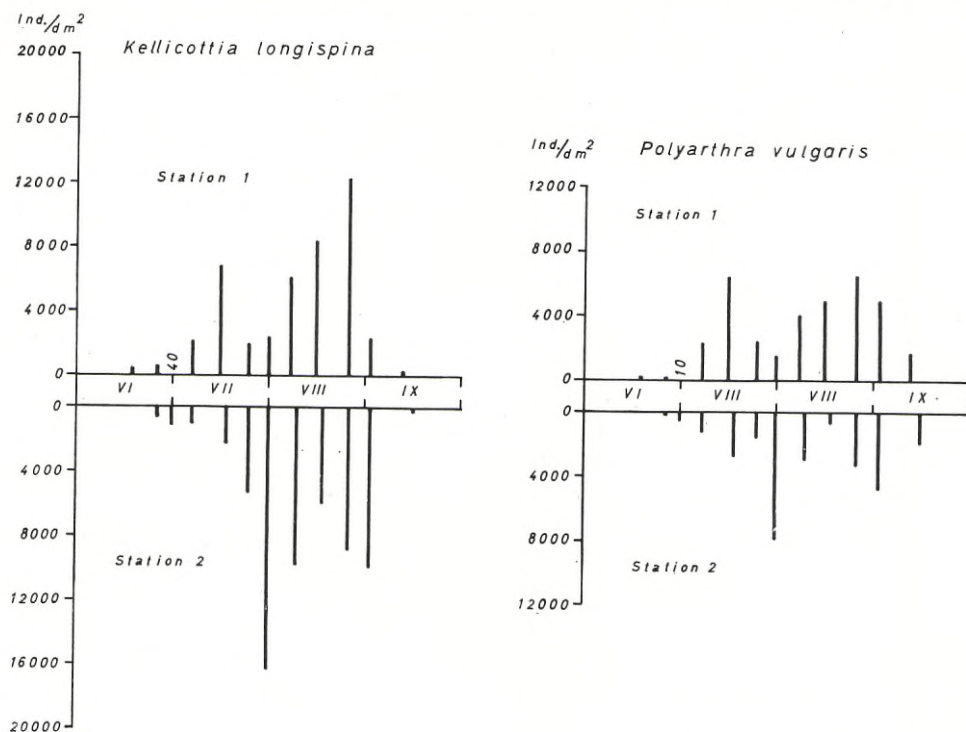


Fig. 4. Variation in the summer standing crop of *Polyarthra vulgaris* and *Kellicottia longispina* in Ransaren in 1958.

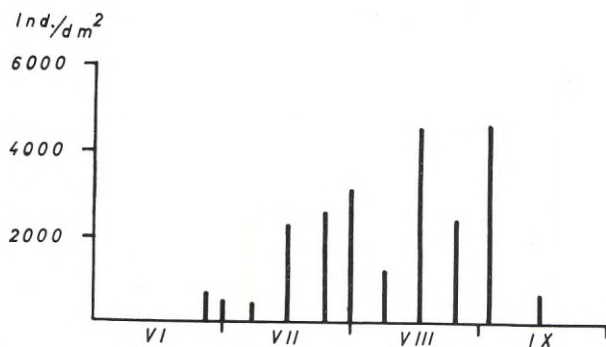


Fig. 5. Variation in the summer standing crop of *Keratella cochlearis*. Mean value for station 1 and 2 in Ransaren in 1958.

and the other at the end of August. The value of August 25th in fig. 5 is no doubt too low and does not represent a minimum. *K. cochlearis* very often occupies the water layers close below the thermocline (in many cases below 10 m) and the maximum vertical densities are not always covered by the samples.

Conochilus unicornis. Very common in both lakes. In summer very high values are often observed, while the population in winter is very

few in numbers. In the samples *C. unicornis* appears in colonies or as solitary individuals. Because of that I have found it very hazardous to base any conclusion upon the quantitative countings. By chance some samples contain more colonies than other and as only a few colonies can make up 100 individuals it might be supposed that the observed values are not comparable. A counting of 10 5-m parallel samples confirmed this suggestion. The following values were obtained: 0, 27, 0, 25, 0, 7, 2, 32, 0, 4. For these reasons I will not in this connection present any diagram of the annual cycle nor give any exact quantitative value for this species but only say that *C. unicornis* has been found in relatively great numbers during the summer and that the population decreases strongly in winter.

Asplanchna priodonta. The abundance of this species varies from year to year. In the years 1954—1956. *A. priodonta* was sparse in both the lakes. In 1957 in Ransaren there was a marked increase in number. In 1958 the population was very sparse and in 1959 once again relatively high values were obtained. The cause of this periodicity is not settled. In Kultsjön the population never fluctuated like this but remained all the time on a very low level.

Synchaeta pectinata and *Synchaeta truncata*. Like *Asplanchna priodonta* both these species reached maximum values during 1957 and 1959, while they in the other years were quite sparse. They occupy different waterlayers, *S. truncata* occurring closer to the bottom than *S. pectinata*. The former species seems to be more adapted to cold water (cf. Pejler 1957).

Filinia terminalis, *Polyarthra dolichoptera* and *Keratella hiemalis*. Cold-stenothermal forms, which occupy the hypolimnion. They occur in varying numbers, *F. terminalis* usually being the most abundant, while *K. hiemalis* is very rare.

Collotheca mutabilis. Regularly found in the summer samples but never in winter.

Ascomorpha saltans. Only found in 1959 and then quite common in Ransaren. A few individuals have also been found in Kultsjön.

Ploesoma hudsonii. This species has been found in small numbers in Kultsjön but never in Ransaren.

Besides the species mentioned above some other rotifers, some of which are not pelagical, have been found in the lakes. They are, however, very rare and the reader is referred to the list of species (page 92).

In this chapter only a few quantitative values have been given. To obtain these the reader is referred to the following chapters and to the tables at the end of this paper. All the quantitative results can not possibly be presented, but I hope that the tables will give a sufficiently good picture of the standing crop of zooplankton in Ransaren and Kultsjön.

IV. The horizontal distribution

The reliability of the quantitative samples has always been a difficult problem for the investigators of lake plankton. Errors in the collection methods might be estimated and limited but the worst error of all, the variations in the animal densities due to changes in the environmental conditions, is very hard to determine. The conditions in the open water are very variable and it will therefore be very risky to extend the results of a series of samples to be valid for times and localities other than where or when the samples were taken. Yet, this has to be done, because almost no planktologist has time or resources enough to take and to work up the number of samples necessary to give a completely reliable statistic material.

The results in this chapter are mainly based on the values from 1958, when the investigation was most intensive. As I deal with the principle factors determining the horizontal distribution in Ransaren the results are also valid for the other years.

When dealing with the distribution of the zooplankton, it is necessary to pay attention to the water movements of the lake. There may be a surface transport of plankton due to the wind action and even in the deeper strata the zooplankton may be irregularly distributed in case of internal seiches. On the basis of the temperature distribution MORTIMER (1952) has made a special study of the water movements in lakes. The biological aspects on different kinds of water movements have been considered by, *inter alia*, DEMOLL (1922), THOMAS (1950) and RAGOTZKIE and BRYSON (1953).

A very good example of the irregular plankton distribution, caused by wind-induced water movements, is presented in fig. 6. The samples were taken on July 1, 1958 at a profile along Ransaren. During the last days of June a period of hot weather brought about a considerable warming of the surface water (fig. 7). This warm water-layer was, however, quite thin and the relatively weak southerly wind that was blowing during the whole period was sufficient to bring all the warm surface water to the northern end of the lake. At station 1 in the southern end cold hypolimnetic water poor in plankton reached the surface. Figure 6 presents the isotherms and the volume of the dominating zooplankters in $\text{mm}^3/5$ l. At station 1 and 2 samples have been taken at the ordinary depths, while at the interjacent localities only the surface water is examined in order not to extend the sampling during too long a time.

The position of the sampling stations within the profile can be seen in fig. 23 (page 126).

All the zooplankton species are affected by the water transport. The very big difference in volumes between station 1 and 2 depends on the richness of crustaceans at the latter station while these as well as the rotifers are very few at station 1. A comparison of the zooplankton volumes in the sur-

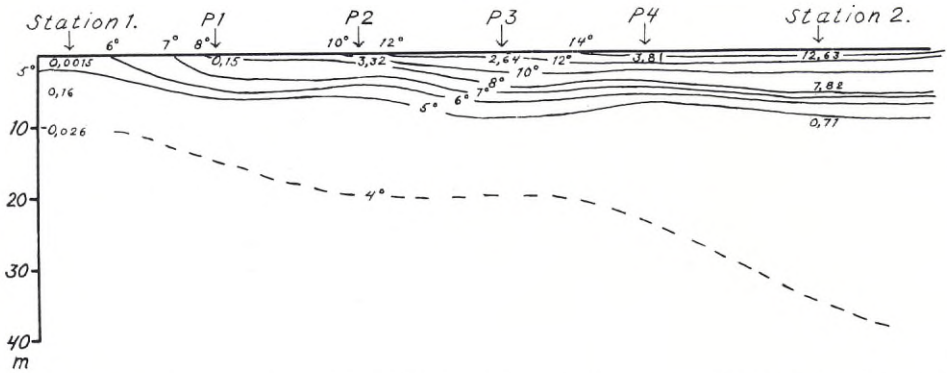


Fig. 6. Isotherms and volumes ($\text{mm}^3/5 \text{ l}$) of the dominating zooplankters in Ransaren July 1, 1958.

face layer (1 m) thus clearly shows a concentration of animals in the northern end of the lake. At station 1 the total volume was $0.0015 \text{ mm}^3/5 \text{ l}$, at P 1 0.15, P 2 3.32, P 3 2.64, P 4 3.81 and at station 2 $12.63 \text{ mm}^3/5 \text{ l}$.

Though the transport of water must be considered to be the primary factor in bringing about a plankton distribution like the one described above, it still remains to explain whether there is a question of a direct or an indirect effect of the water movements. I have already touched upon this problem on page 98 and when I now deal with the horizontal distribution there is need for a further discussion.

On page 98 the question was raised, whether a wind that is blowing from the same direction during a period that is long enough to cover a significant increase in the plankton, might produce zones of different productivity in opposite ends of a lake. If the wind is blowing without interruption both day and night this is no doubt the case. Cool bottom water will continuously reach the surface in one end of the lake and becomes gradually heated during the horizontal transport towards the other end. This warming effect is maximal in small shallow lakes, which during the warmest period of the summer do not show a thermal stratification (epilimnic lakes, ALSTERBERG 1935). However, in a deep mountain lake of the stratified type hot weather together with long-lasting winds from one direction is only capable of heating the upper layers of the water volume and such a lake never becomes horizontally homothermal under the conditions described above.

Returning to the discussion of the most productive zones in Ransaren I have already stated that such may be formed when the wind is continually blowing from one direction both day and night. Yet southerly winds together with fine weather most often weaken in the evening and at night calm often prevails. It is therefore necessary to pay attention to the internal waves that may arise during calm conditions. I find it unnecessary here to describe

the well-known phenomenon of the origin of internal waves or seiches, which is familiar to every limnologist. I will only mention that the vertical oscillations of the water layers is followed by a simultaneous horizontal transport of water. When speaking for instance of the stratum of the thermocline this implies that when the thermocline is moved from its uppermost to its lowest level at one end of the lake the warm surface water that has been brought away by the wind floats back to the same end. If the oscillation of the strata is rapid enough to change the thermal picture during one night with calm weather, lasting productive-centres of thermal origin cannot arise. It is thus necessary to know the oscillation period.

Knowing the position of the thermocline and the densities of the upper and lower strata it is possible to determine the approximate periods of oscillation by the formula by STOKES and WATSON (MORTIMER 1953). This has been done on some occasions in 1958, which resulted in the following values. A total oscillation of the internal seiches was completed within 65 hours on June 30, 94 hours on July 31 and within 46 hours on August 19. This means that during the periods of southerly winds in the shifts of months June—July and July—August the swinging of the thermocline was too slow to allow any considerable backward movement of the warm surface water during the calm night. The conditions for the origination of a lasting favourable zone in the northern end of the lake are thus fulfilled. In the inter-jacent period strong northerly winds were blowing, which only weakened inconsiderably in the night-time. The result was a constant flow of surface water in southerly direction. During August the prevailing winds were from the south. The water movements of the internal waves were quite fast, but the relatively deep position of the thermocline (about 10—15 m) brought about that the upper turn of the oscillating thermocline was reached 5—10 m below surface. Hypolimnic water never reached the surface, which was the case in July when epilimnion was very thin.

From these observations we notice that the horizontal distribution of the plankton is very dependent on the weather conditions during the first part of the summer when the lake is thermally stratified only in the superficial strata, while later in the summer not even a continuous wind can bring the whole epilimnetic water-mass towards one end of the lake. Because of the high zooplankton densities in late summer the differences in the number of individuals at the opposite stations 1 and 2 can be greater than in early summer, but the percentage difference is always considerably less (see table appendix at the end of the paper).

Above I have only spoken of the irregularities in the horizontal distribution of zooplankton that might be due to a transport of epilimnic water. It is true that this is the most important factor, as most of the common plankton animals prefer the water of the epilimnion. Yet, occasionally they are spread into the hypolimnion almost down to the bottom, which was a com-

mon case in 1958. Others such as nauplii and copepodites of *Cyclops scutifer* and the rotifer *Keratella cochlearis* regularly develop their maxima in the region below the thermocline in late summer. When dealing with the horizontal distribution it is thus necessary also to study the vertical distribution of the species and to take into consideration the horizontal water movements in the hypolimnion in the case of standing waves, as a wind-induced surface current is accompanied by an opposite current in the hypolimnion of the same magnitude.

Now, after dealing with the principal scheme of horizontal water movements in Ransaren I shall, on the basis of these considerations, treat the distribution of the most abundant zooplankton species in Ransaren in the summer of 1958. Such a treatment of the material is inevitably necessary in order to be able to judge the reliability of the quantitative samples of the other years, when the investigation was less intensive and the main material was from station 1 only. Knowing the way in which the water movements may affect the distribution of the species and also knowing the weather conditions and water temperature of a sampling period it is possible, in the case of surprisingly high or low values, to avoid confusion of normal changes with the effect of the regulation of the lake.

In fig. 7 a simplified scheme of the water temperature and wind conditions is presented. Because of the directing effect of the mountains most winds of importance for Ransaren give rise to waves, travelling in either direction of the long axis of the valley. Winds blowing from a direction between W and NE are thus called northerly winds while those, which are blowing from SW to E are termed southerly winds.

In fig. 8 the quantitative values of the following species are given: nauplii, copepodites, and adults of *Cyclops scutifer*, juveniles and adults of *Daphnia galeata* (not separated in the diagram) and the rotifers *Polyarthra vulgaris*, *Kellicottia longispina* and *Keratella cochlearis*. Adults of *Cyclops scutifer* as well as other zooplankton species, with the exception of *Conochilus unicornis* (cf. page 100) are too few to allow any conclusion concerning their horizontal distribution.

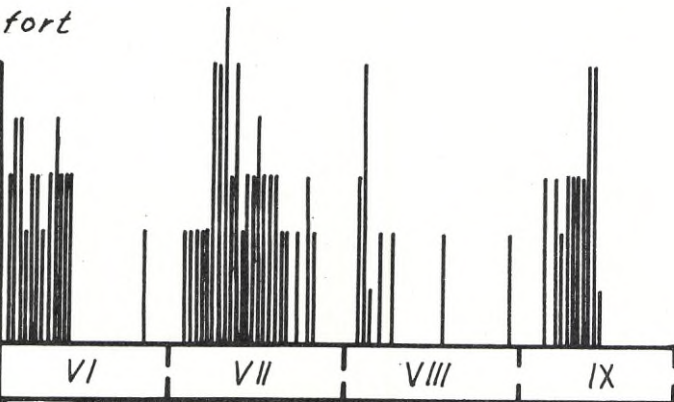
In the beginning of the ice-free season there are no significant differences between station 1 and 2. The low water temperature limits the growth and the whole lake is circulating in a homothermal condition. In the end of June and in the beginning of July the first marked differences appear, which are already described in the beginning of this chapter. I have also pointed out, that during this period with southerly winds and relatively hot weather the pre-requisite conditions are fulfilled for a formation of a horizontal zonation of the warm productive surface water. I therefore conclude that the high values, that were obtained at station 2 compared with those at station 1, are not entirely a result of a transport of already existing animals, but they are also caused by a higher growth-rate within this warmer part of the lake.

Winds

W-N-NE

Beaufort

5
4
3
2
1
1
2
3
4
5



SW-S-E

Temperature

29/8 4 6 8 10 12°C 4 6 8 10 12°C

17/8

31/7

17/7

30/6

10

20

30

40

m

m

Station 1.

Station 2.

Fig. 7. Water temperature and wind conditions in Ransaren in the summer of 1958.

During the period of strong NW winds in July the stratification was practically broken down. On the 24th (not on the diagram) the temperature difference between surface and bottom was only about 1° at both the stations. The surface temperature was 7.7° at station 1 and 7.5° at station 2. Because of the continuous NW wind higher values were found at station 1 in the middle of the month. During the last ten days of July a new period with S winds set in. The expected change in the dominance of the stations during this period is verified by the quantitative values of the 24th with the exception of nauplii of *Cyclops* and *Keratella cochlearis*. The disagreement between these two and the other species is still more accentuated in the shift of the month and may be explained by the different vertical distribution. The values from the July 31 and from the August 1 show considerably higher values at station 2 for all the species but those which prefer the deep layers. Both *Keratella cochlearis* and nauplii of *Cyclops* very often develop their maxima below the thermocline and avoid the surface water (cf. chapter V.) and as the water column at station 1 is almost entirely made up of water from the deeper strata on this occasion the discrepancy between the horizontal distribution of the species is in good agreement with the supposed effect of the water movements.

During August the situation is not so simple. The dominating winds are from the south, but they are occasionally interrupted by short periods of north-westerly winds. The differences between the opposite ends of the lake seem at the first glance to be a result by chance, but a study of the probable water movements together with the vertical distribution makes it possible to clear up the problem. As to the development of *Cyclops* and *Keratella* there is not much to say. The course of development is the same at both the stations and the differences in the number of ind/m² can easily be explained by the prevailing winds and the vertical distribution. The population of *Daphnia galeata* declines rapidly during August in the whole lake and already in the middle of the month the number of individuals is too small for an investigation of this kind. The remaining two species *Polyarthra vulgaris* and *Kellicottia longispina* on the other hand are numerous and show a very interesting distribution.

Remarkably enough these two rotifers always show coincident maxima and minima though they may compete for food. They can therefore advantageously be treated together. When the diagram in fig. 8 was first drawn I was surprised to find, that though the wind during August was preponderatingly from the south the highest values were found at station 1. Such a distribution was definitely contradictory to what was to be expected for epilimnic species. It was therefore necessary to deal thoroughly with all the data that was known of the rotifers and the environmental conditions that were prevailing during the periods when the samples were taken. There are three sampling days that are of special interest, namely the 15th and

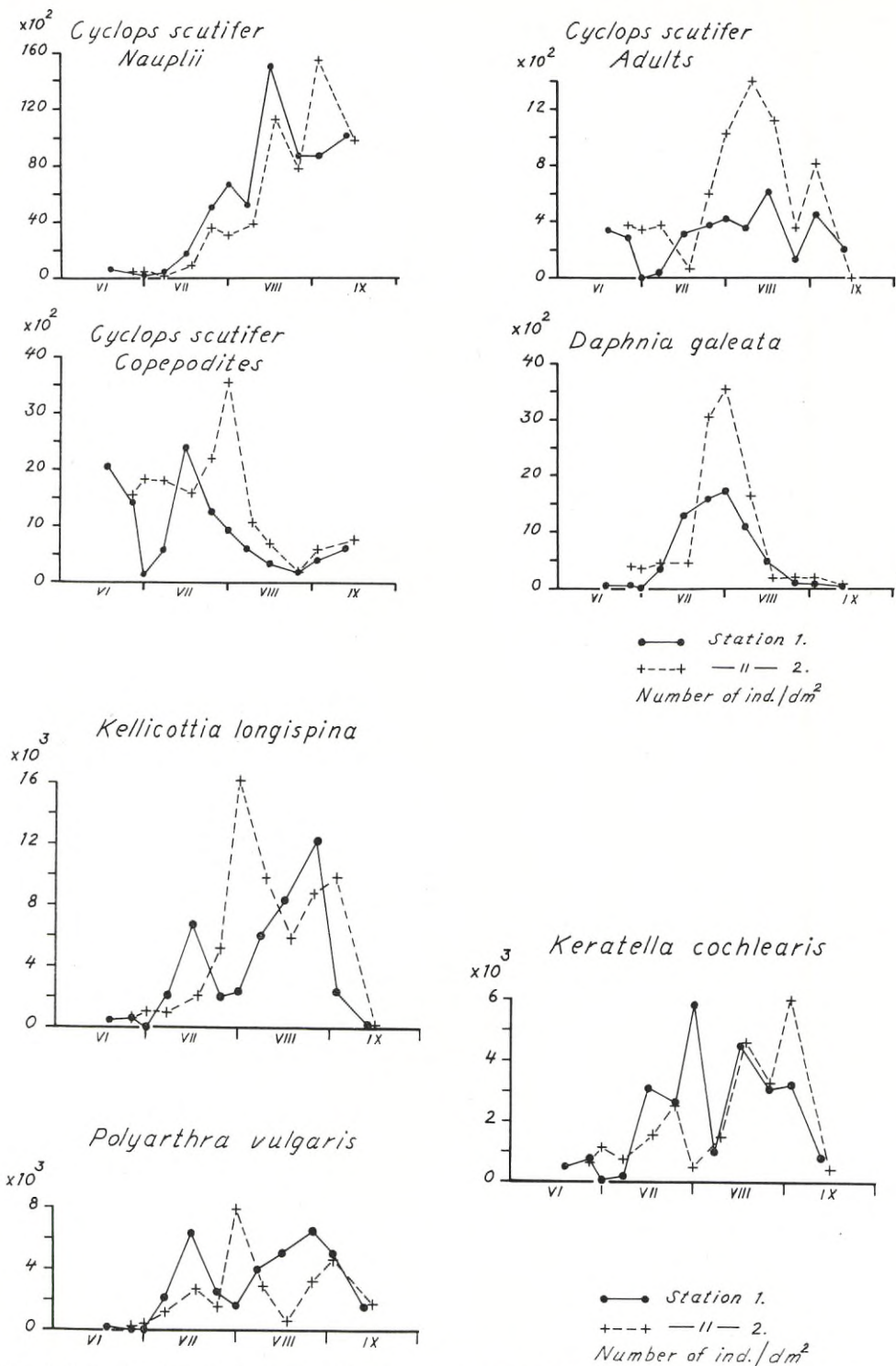


Fig. 8. The abundance of some zooplankton species at station 1 and 2 in Ransaren in the summer of 1958.

Table 4. Ind./dm².

Depth m	Station 1				Station 2			
	15.VIII		25.VIII		17.VIII		25.VIII	
	P	K	P	K	P	K	P	K
1	95	112	306	536	32	106	104	394
5	170	202	261	613	6	129	177	469
10	22	56	40 ¹	110 ¹	9	71	26	85
20	75	123	45	48	4	95	9	16
40	10	63	23	35	7	8	14	25

P=Polyarthra. K=Kellicottia.

¹ Calculated values.

25th at station 1 and the 17th and 25th at station 2. In table 4 the quantitative values for the vertical series are given.

I find it unnecessary here to describe all my speculations about this problem. I can only state, that every attempt to explain the distribution by means of a direct transport of animals has completely failed. This seems to upset the whole discussion above, but that is however not the case. During the summer the rotifers are able to develop at least two maxima succeeding each other (cf. page 98—99). If no winds were acting, no horizontal differences could be expected provided that the lake is homogenous from the productivity point of view. Yet, above I have tried to show that a steady wind may locate the productive water strata in one end of the lake and that this location can remain for a period, the length of which is dependent on the weather conditions. I have also shown that such a period began during the last days of July and resulted in a concentration of animals at station 2 in the shift of the months. The dominance by southern winds during August prevented an equalization over the whole lake. It is my opinion, that not even short intermissions of the south winds were able to transport any considerable volume of the epilimnic water back to the southern end. Under these circumstances it is to be expected that the rotifer population at station 2 may gradually decline due to too high a population density and that a new maximum may appear if the conditions once more become favourable, which seemed to be the case in 1958. It is very likely that the high zooplankton densities at station 2 in the end of July caused a lack of food in the northern end of the lake which in turn affected the reproduction of the species. On the 31st of July 11.6 % of the *Kellicottia* females were carrying eggs and on the 9th of August this figure declined to 9.1 %. During the same time the number of oviparous females at station 1 increased from 4.5 to 20.0 % and reached a value of 41.0 % in the middle of August. At this time the corresponding value at station 2 was 20.0 %, an increase which is in agreement with the curve of the standing crop of *Kellicottia*.

At station 1 the number of individuals was on a low level during the first days of August due to the southerly winds. During the following days the water temperature gradually rose and even this part of the lake became thermally stratified. Though the upper part of the water column was colder than at station 2, the conditions became favourable enough to make possible a quite rapid growth. There was, however, a constant loss due to the transport of surface water in northerly direction, which is also confirmed by the fact that the minimum at station 2 is on a relatively high level. The maximum values at station 1 were obtained as late as on the 25th and after the decline of the population in the beginning of September the environmental conditions were not favourable for the development of a new population of any considerable magnitude.

On the 2nd of September the values for the nauplii of *Cyclops* were found almost twice as high at station 2 than at station 1. The very weak wind can not possibly be responsible for this distribution and above I have shown that the nauplii prefer the deeper layers and may be transported in a direction that is opposite to the wind. I find no reasonable explanation for the dominance at station 2. It is therefore my opinion that this value is not a true value, but is caused by the necessary limitation of the sampling method. The samples from the deep layers are very scarce and I will point out that the quantitative values for a species with maximum below the thermocline may occasionally be too low or too high depending on the exact position of the maximum.

In order to further check the validity of the discussion above I have compared the distribution of the zooplankton with the standing crop of their food-algae and the production of the whole phytoplankton (RODHE and NAUWERCK, in manuscript). The algae are still more affected by water movements than are the zooplankton. The diagram of the standing crop of algae in fig. 9 compared with that of the least movable zooplankters, namely the rotifers, shows an almost complete agreement in the development of the epilimnic species. This agreement indicates that both the phytoplankton and the zooplankton are affected by a factor acting in the same way on both and this confirms strongly the theory of the wind effect as the main factor controlling the distribution of the whole plankton community. Concerning the sampling of phytoplankton only three vertical series have been taken at station 2 and the dates of these series fall within periods of marked southerly winds. The standing crop is considerably higher at station 2 and so is also the production. The higher production at station 2 on these occasions proves further that the differences are not entirely depending on a transport of organisms, but to a great extent on the translocation of water-masses, where the environmental conditions are favourable for the growth of plankton. Unfortunately no phytoplankton samples from both the stations have been taken during a period of northerly winds. However, the most important

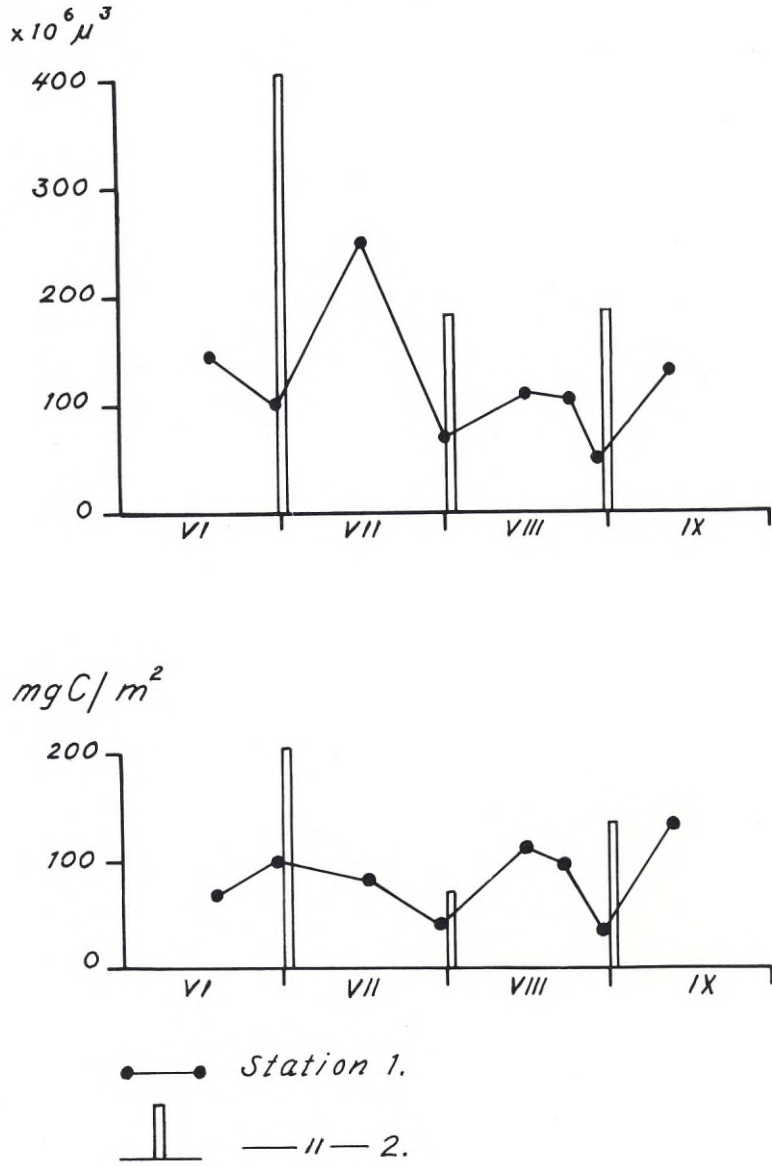


Fig. 9. Standing crop of some phytoplankton groups (above) and primary production (below) in Ransaren in 1958.

period of such winds was in the middle of July and at that time the highest phytoplankton values at station 1 were found. The water temperature was low, the weather was preponderantly cloudy and the phytoplankton production was quite low. Thus in spite of quite a low production and a grazing standing crop of zooplankton the highest phytoplankton values of the whole summer were observed. Together with the zooplankton observations in 1958 this implies that a previously supposed theory of more productive conditions in the northern end of Ransaren is not settled. This theory was mainly based on the dominance of cladocerans at station 2, but the material was too small to allow any true conclusions. However, also in the summer of 1957 there was a dominance especially of *Daphnia galeata* at station 2 and as the species is much more abundant in this year and provides a better material, this dominance has to be explained. As the population of *Daphnia* appears in the greatest number from the middle of July to the middle of August this period is of the greatest interest. The diagram of the wind conditions during this year (fig. 32) shows that the wind was mainly from a southerly direction during the whole period except for 4 days in the beginning of August. The dominance at station 2 may thus even that year be explained by the horizontal transport of water. In 1959, however, the highest values of *Daphnia* observed at station 1 were on the 20th of July and the wind was blowing from a northerly direction.

As the shores at the northern end of Ransaren are very flat compared to the southern end, a larger area of land will be submerged when the water level rises, due to the regulation. The greatest regulation effects are thus to be expected in this area and it would not be surprising to obtain higher plankton values at station 2. As I have shown above the differences between station 1 and 2 are very well explained by the wind conditions and I therefore conclude that if the effects of the regulation act upon the lake unequally in different parts, this is not illustrated by the zooplankton distribution. In this connection I deal only with the regulation effects on the organisms in the pelagical zone.

In 1958 some vertical series were taken at station 3 in the bay of Fabmeluokte at the northern end of Ransaren. The bay is relatively shallow. The samples were taken at a depth of 20 m and therefore the values are not easy to compare with those from station 1 and 2. Nor are the values representative for the pelagical zone, because of the shallow water and the protected position of the bay. In fig. 10 the observed quantitative values are presented. A comparison with the layers between 0—20 m at station 2 indicates that the bay is more similar to this station than to station 1 and that especially southerly winds affect the plankton densities by concentrating the animals in this area. Unfortunately values are missing from the shift of the months July—August, when top values were obtained at station 2. In fig. 10 no line has therefore been drawn between the last sampling date of July and the

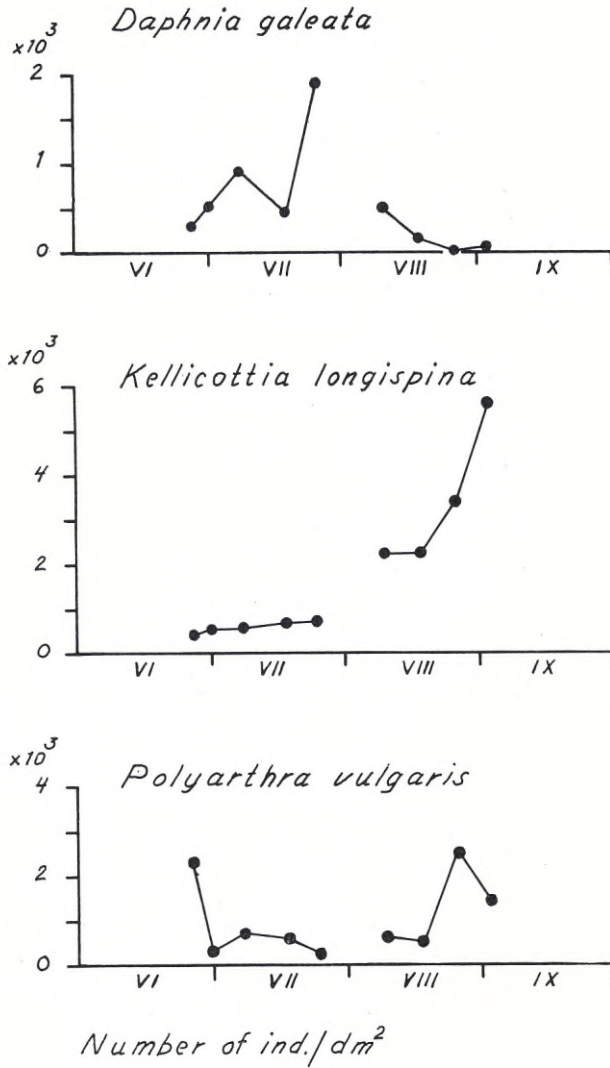


Fig. 10. Standing crop of *Daphnia galeata*, *Kellicottia longispina* and *Polyarthra vulgaris* at station 3 in Ransaren in 1958.

first one of August. The bay of Fabmeluokte was investigated mainly to observe whether this area was or was not diverging from the rest of the lake and though the values are not easy to compare no marked differences have been observed between station 3 on one hand and station 1 and 2 on the other.

I will end this chapter by pointing out once more, that in order to obtain a reliable zooplankton material from a lake it is inevitably necessary to sample in at least two opposite parts of the lake and also to know the thermal conditions during a number of days before the sampling periods. Knowing the principle scheme of the horizontal localization of plankton it is possible approximately to eliminate some errors in case of only one sampling station.

V. The vertical distribution

The collected material gives a good picture of the vertical distribution of the zooplankton. The necessity of limiting the number of vertical samples in every series is to a great extent compensated through the increased number of series that, thanks to this, have been possible to take.

Most species are epilimnic. This, however, does not mean that they are restricted to the water-layers above the thermocline. As a matter of fact high values are often obtained also in the bottom water but animals living there are often in a very bad condition and will soon be deposited on the bottom. In the metalimnion many species reach their maximum densities. A few species are almost entirely restricted to the hypolimnion. The hypolimnic species are cold-stenothermal winter forms, which during the winter occupy the whole water-body.

It is thus possible to distinguish epilimnic and hypolimnic species on the basis of the different temperature dependence of the species. However, many other factors sway the vertical distribution, such as oxygen deficiency, light and perhaps the most important: the vertical position of the food-layers. In Ransaren and Kultsjön oxygen is never a limiting factor. The values are never below 7 mg/l, but most often vary between 9—11 mg/l. The response against different light conditions is best illustrated by the diurnal migration of the zooplankton. This phenomenon is most pronounced among the crustaceans which are more active swimmers than the rotifers. In 1957 and 1958 series have been taken in Ransaren with an interval of only a few hours in order to study the diurnal migration of the species. However, the only species among the crustaceans that was numerous enough to allow the drawing of a diagram was *Cyclops scutifer* (fig. 11).

At all times the majority of the animals was found between the surface and a depth of 10 m. Within this layer diurnal changes can be seen in the vertical position of maximum population densities. The tendency is, how-

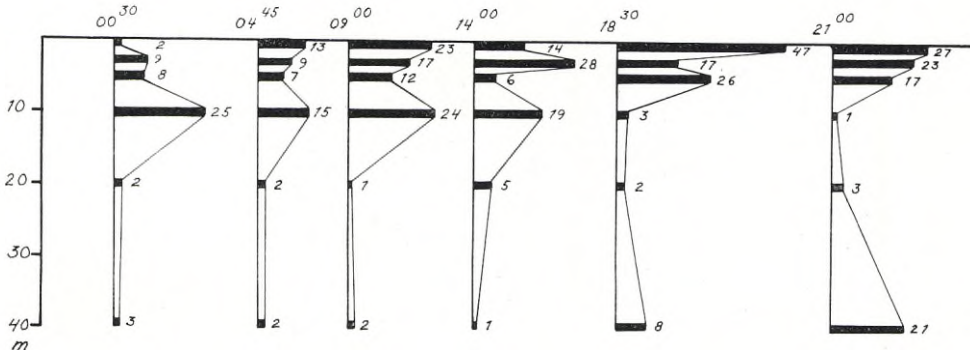


Fig. 11. Vertical distribution of *Cyclops scutifer* in Ransaren station 1 on August 19, 1958.

ever, quite diffuse so I have to rest satisfied by saying that there seems to be an upward movement in the evening when the highest values of the surface water were observed.

Simultaneously with the sampling of zooplankton on the 19th of August, 1958, temperature measurements were made by my fellow-worker R. RAGNBERG. This material, which has been left at my disposal, reveals the very close connection between the vertical distribution of the zooplankton and the thermal conditions of the lake. In the daytime on the 18th a moderate north-westerly wind was blowing. This wind decreased in the afternoon and in the evening the weather was calm. The wind, however, was strong enough to cause an internal seiche after the fall of the wind. In this case, the thermocline was forced upwards at station 1 meaning an increment of the hypolimnion and a corresponding decrease involving epilimnion. During the course of nine hours the vertical position of the thermocline changed from 17.7 m at midnight to 7 m at nine o'clock p.m. the following day. In fig. 12 a curve of the position of the thermocline has been drawn together with curves showing the position of nauplii of *Cyclops scutifer*, *Kellicottia longispina* and *Polyarthra vulgaris*. The plankton curves show the depth at which the animals in question start to develop their maximum abundance. The points plotted on the curves represent the inflexion-point on the part of the curves where there is a maximum increase respectively decrease in the number of individuals (below to the right in the figure). In Ransaren both rotifers have an epilimnic distribution while nauplii of *Cyclops scutifer* show a tendency to prefer the water-layers below the thermocline. This implies that in the first two cases the drawn curves represent a lower limit for maximum abundance while in the latter case the curve illustrates the upper limit.

The most striking result is the very good correspondence between the displacement of the thermocline and the vertical position of the zooplankton. The thermocline seems to be an effective boundary below which *Kellicottia longispina* and *Polyarthra vulgaris* are very few in number. The limiting effect of the thermocline on nauplii of *Cyclops* is the reverse. The number of individuals decreases rapidly above the thermocline. The results show that the light condition of the water is a very subordinate factor. The animals occupy a water layer where the primary factors food and temperature are favourable. A vertical displacement of these "optimal" layers brings about a corresponding transposition of the plankton animals. The inherent migratory qualities in order to react against changes in the light conditions might thus be suppressed by the necessity to remain within the water-layers where more important factors than light are favourable. The rôle of the light conditions must, however, not be ignored, but it is my opinion that the diurnal migration is restricted to take place only within the food-layer of the species in question. In fig. 12 the ascension of the plankton curves

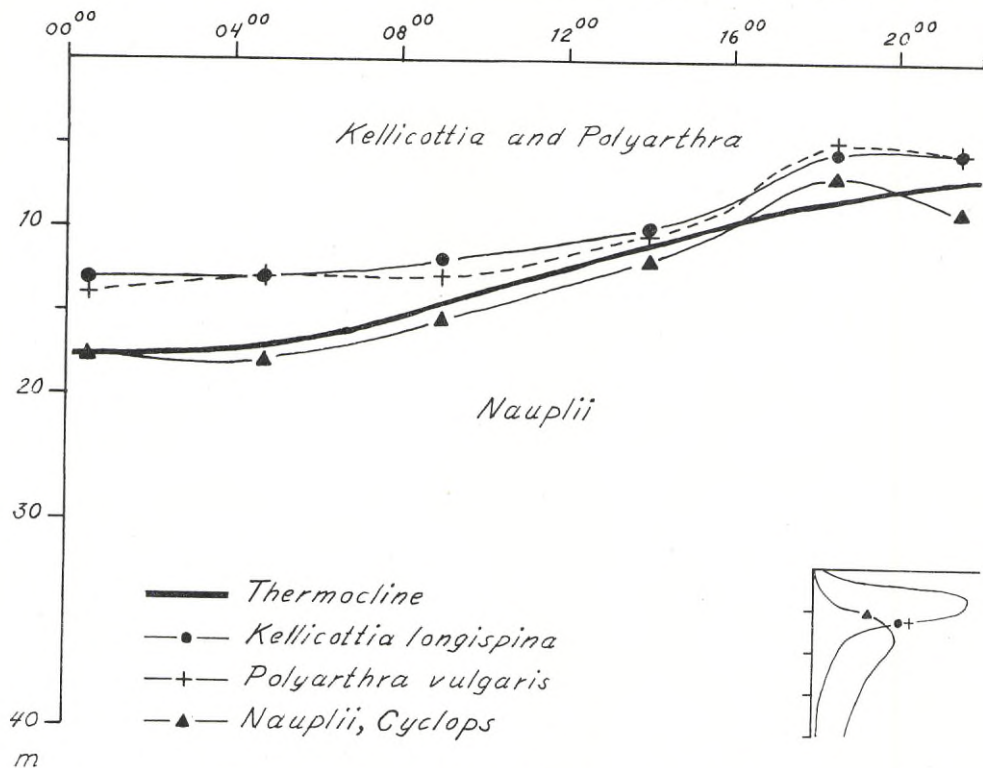


Fig. 12. Vertical position of the thermocline in Ransaren at station 1 on August 19 1958 together with the position of *Kellicottia longispina*, *Polyarthra vulgaris* and nauplii of *Cyclops scutifer*. (For explanation see text.)

between 4 and 9 a.m. indicates that there is an upward movement of the animals that is more rapid than would have been the case if the vertical water transport alone was operating.

I have in this paper already discussed the reliability of the zooplankton samples. The question of the vertical distribution provides another example of how many factors must be known in order to get reliable results. Without temperature measurements both day and night one cannot determine migratory rates and distances. Nor is it possible to determine any fixed depth at which a population seems to be most abundant, because this depth varies with the water movements. However, if the position of the thermocline is known on each occasion it is possible to determine whether a species prefers the surface water, the region above or below the thermocline, respectively the bottom water. Any attempt to determine a fixed depth favourable for a population within the whole epi- or hypolimnion of a lake seems to me to be waste time. Very uncertain is also the commonly used method of constructing depth-time diagrams of temperature and plankton

organisms especially when there is an interval of 10 days or more between the sampling periods. The results from fig. 12 clearly show that vertical changes of 10 m may occur within 24 hours.

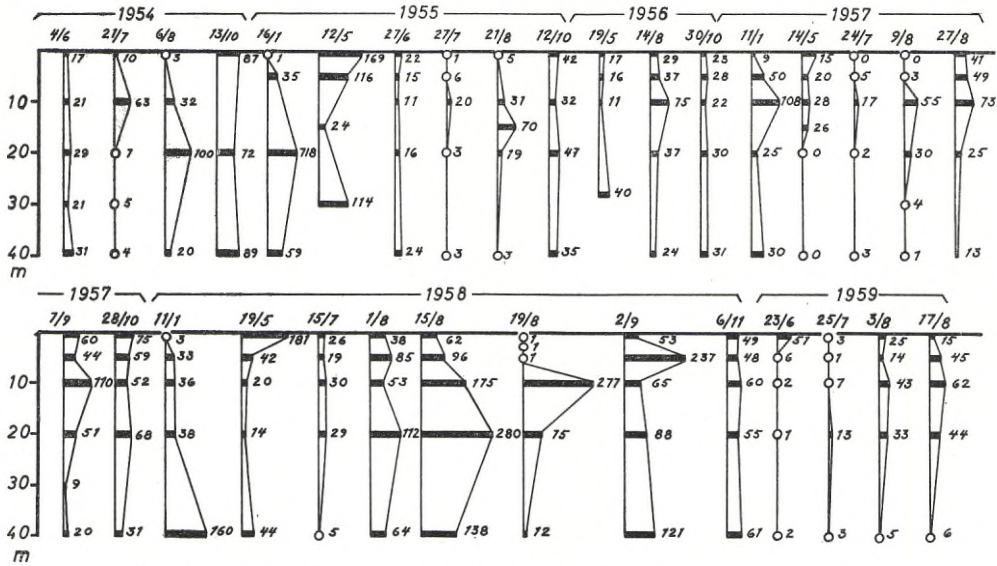
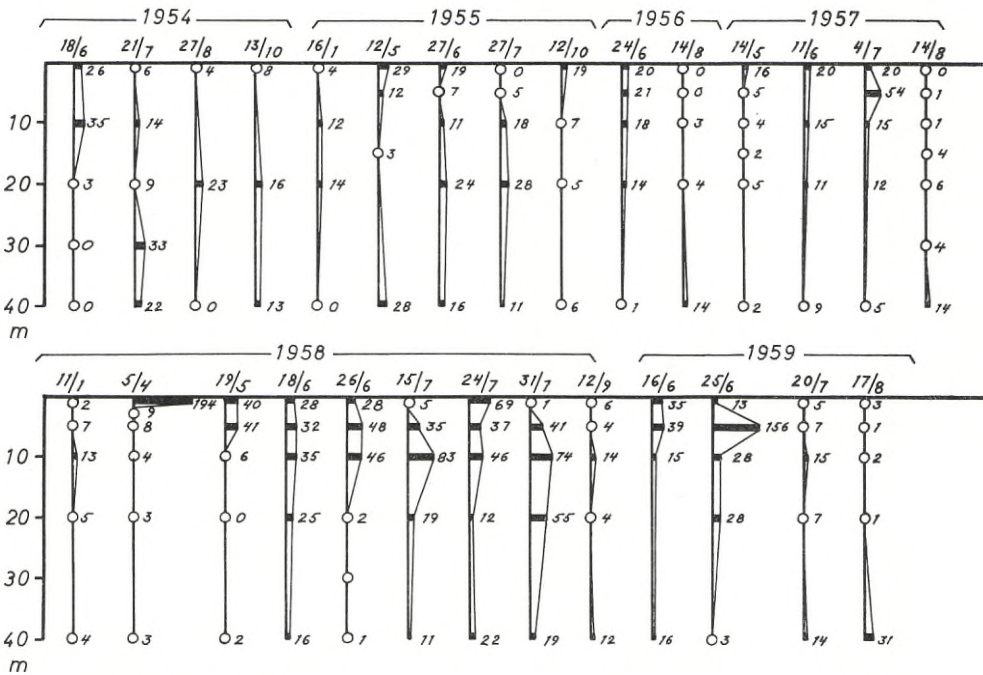
Bearing these considerations in mind, I will try to discuss the vertical distribution of the zooplankton species in Ransaren and Kultsjön. No marked difference between Ransaren and Kultsjön has been observed. It is therefore not necessary to deal with both the lakes. The results from Ransaren are valid also for Kultsjön. Thus the only species that are discussed from the material of Kultsjön, are those which do not occur in Ransaren.

The following principal scheme is common to all the zooplankton species. In summer the animals can be found within such water layers as correspond to the environmental demands of the species in question. Most probably the temperature is the most important factor, which means that eurythermal species may occur in the whole water body while cold-stenothermal species are restricted to the hypolimnion. As a rule the highest densities are found between 1—10 m, that is to say the trophogenic layer. During the autumn turnover the stratification of the zooplankton is broken down and no marked differences between surface and bottom water are obtained. During the reversed thermal stratification in winter the conditions are different. During midwinter when the days are very short and the standing crop of autotrophic phytoplankters is very small there is no need for the animals to occupy the superficial water layers. They most probably feed upon heterotrophic algae and maximum values are often obtained in the lower strata. When the days grow longer in spring and the ice-cover transmits the light, the conditions become favourable for a rapid growth of phytoplankters. In this trophogenic layer immediately beneath the ice a concentration of zooplankton can be found (April 5, 1958, fig. 14, 19, 20). In the May samples an hour-glass-shaped vertical distribution is sometimes found, with a maximum in the surface water and in the bottom water. The surface maximum is already explained above. The concentration of animals in the bottom water may be due to an accumulation of detritus, falling down from above, on which the animals feed. In the interjacent layers the available food is probably too small to support more than a small number of zooplankters.

After the breaking up of the ice, the spring turnover stirs the water and no lasting zooplankton stratification can remain until the summer stratification begins.

In the following I will deal with the vertical distribution during the summer. In the figures only a few vertical series are given. I have tried to choose series of different types and the figures thus give a representative picture of the vertical distribution of the species.

Cyclops scutifer (fig. 13—15). The nauplii avoid the surface water and maximum values are often found close below the thermocline. Though quite high values can be found in the epilimnion a great number of individuals

Fig. 13. Vertical distribution of the nauplii of *Cyclops scutifer*. (ind./5 l)Fig. 14. Vertical distribution of the copepodites of *Cyclops scutifer*. (ind./5 l)

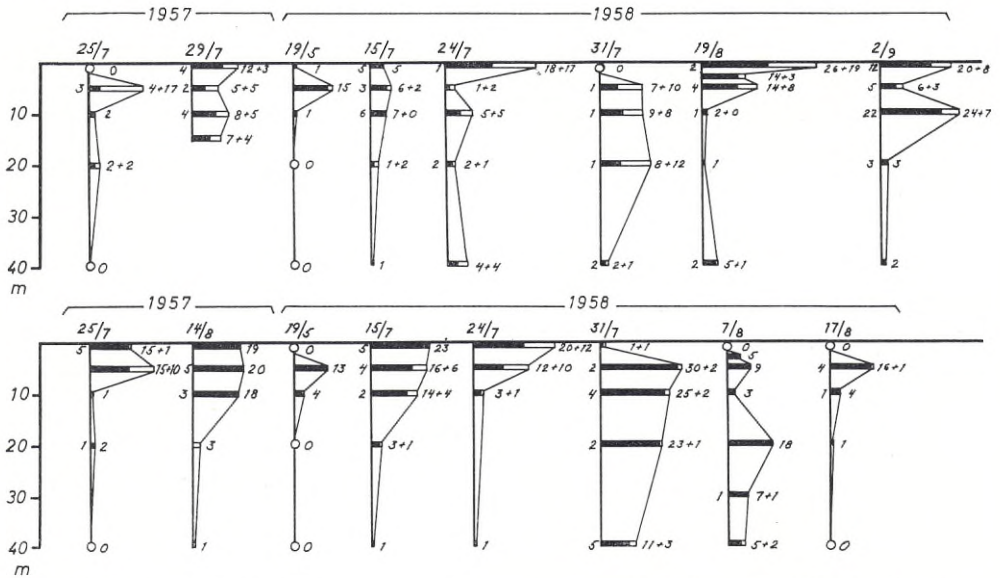


Fig. 15. Vertical distribution of the adults of *Cyclops scutifer* (above) and *Daphnia galeata* (below). ■ = females, □ = males. The figures to the left of the vertical lines represent egg-carrying females. (ind./5 l)

are often found even close to the bottom. The copepodites of *Cyclops* seem to inhabit the same water layers as the nauplii.

The adults of *Cyclops scutifer* differ from the nauplii and the copepodites in their vertical distribution. Maximum is often found close to the surface. There seems to be no difference between males and females. Nor can I find any difference between egg-carrying and not egg-carrying females. The increased weight of the oviparous females does not seem to influence the vertical distribution of the animals.

Diaptomus laticeps (fig. 16). The development of the nauplii is finished when the summer stagnation begins and the vertical position of the nauplii from the May samples is a typical spring distribution with maxima in the surface water below the ice.

The copepodites of *Diaptomus laticeps* develop during June and during that time they prefer the water of the thin epilimnion. On some occasions they can also be found in quite deep layers, but they will never go as deep as the nauplii of *Cyclops*.

The vertical maxima of the adults are frequently found between 5—20 m. The region above the thermocline may be considered the most favourable. There is no difference between the distribution of males and females.

Diaptomus graciloides (fig. 16). The nauplii show a very irregular vertical distribution. Maximum values are sometimes found near the surface and

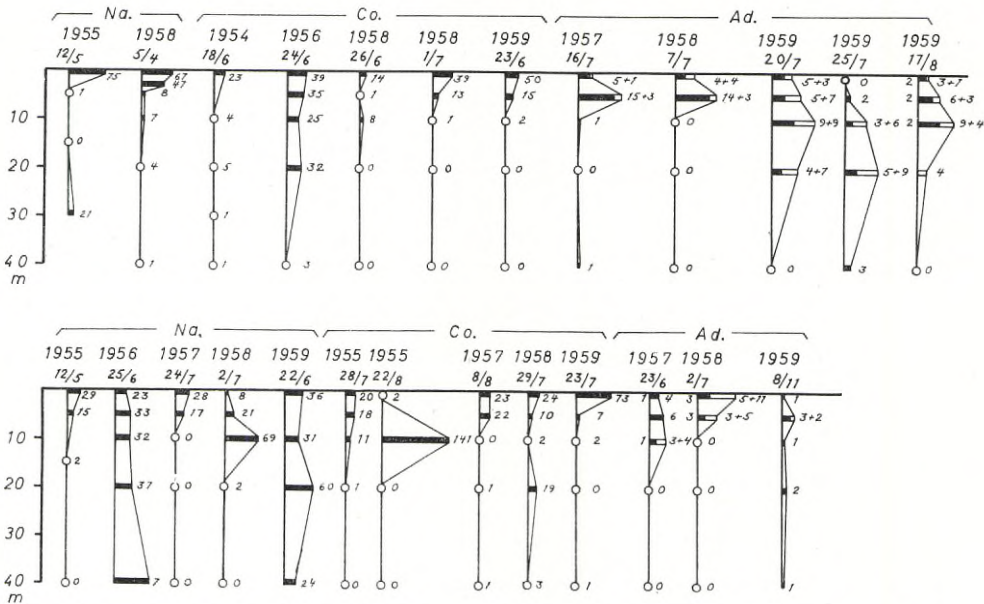


Fig. 16. Vertical distribution of *Diaptomus laticeps* (above) and *Diaptomus graciloides* (below). Na=nauplii, Co=copepodites, Ad=adults, □=males, ■=females (ind./5 l)

on some other occasions at a depth of 10—20 m. In June when the thermal stratification is very weak the nauplii may also be quite uniformly distributed in the whole water column.

The copepodites are very often found near the surface, but maxima may also appear in the region of the thermocline. The very pronounced maximum at a depth of 10 m on the 22th of August 1955 is most probably depending on the presence of swarms of almost adult animals.

In only a few vertical series were the adults numerous enough to allow any conclusions of the distribution. However, the optimal layers are situated between the surface and the thermocline and only a few individuals have been found in the deeper strata.

Daphnia galeata (fig. 15 below). No marked difference between juvenils and adults has been observed. In the figure only adult animals have been plotted. Most often one finds the highest values in the epilimnion, and maxima are often developed close to the surface. In Ransaren in 1958 high values were also observed in the deep layers. No significant difference seems to exist between the distribution of males and females, but there is a slight tendency for the males to occur a little deeper than the females. Egg-carrying females occupy the same layers as the other females.

Bosmina obtusirostris, next to *Daphnia* the most common member of the Cladocerans in the pelagical zone. However the species prefers the near-shore water and I will therefore treat the vertical distribution of

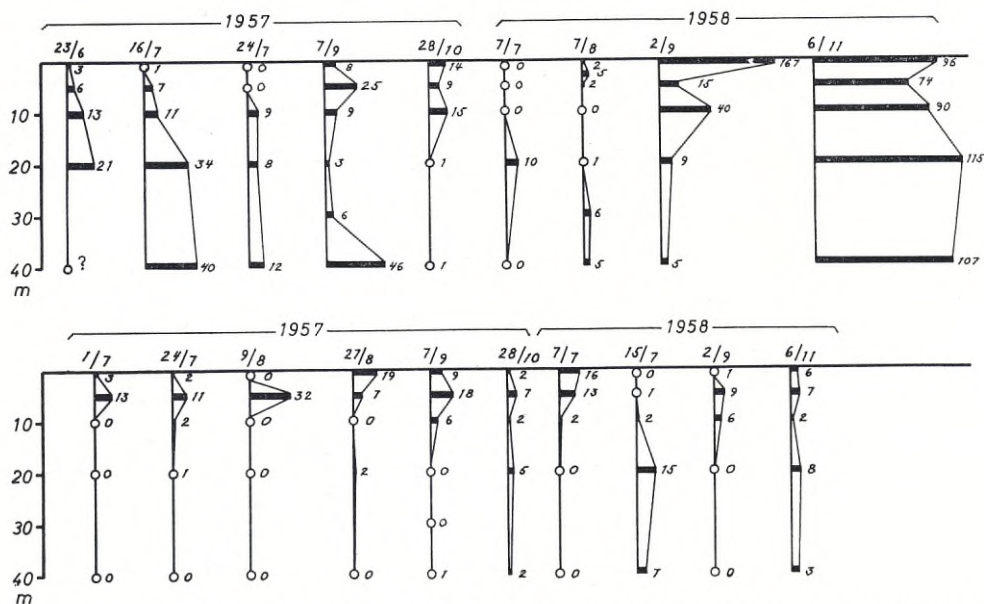


Fig. 17. Vertical distribution of *Synchaeta truncata* (above) and *pectinata* (below). (ind./5 l)

Bosmina in the next chapter where I deal with the zooplankton of the littoral zone.

The other Cladocerans are not dealt with because of the insufficient numbers in which they occur.

Synchaeta truncata and *pectinata* (fig. 17). The former which is considered to be a cold-stenothermal species is common in the hypolimnion. Maximum values are often obtained in the bottom water.

Synchaeta pectinata is regularly found in the epilimnion all the summer. The two *Synchaeta* species thus inhabit different water layers. The recorded presence of *Synchaeta truncata* in the surface water and *Synchaeta pectinata* in the deep layers in some of the series may to some extent be explained by the difficulty to separate small individuals of *pectinata* from *truncata*.

Polyarthra vulgaris and *dolichoptera* (fig. 18). The eurythermal *P. vulgaris* occupies the relatively warm water of the epilimnion and maxima are frequently found at the surface.

Some specimens of *P. vulgaris* are regularly found in the bottom samples but in 1958 and 1959 *P. dolichoptera* was dominating in these samples. *P. dolichoptera* is strictly cold-stenothermal and is seldom observed near the surface in summer. In 1959 the population of *P. vulgaris* decreased rapidly in July to be succeeded by a remarkably rich population of *P. dolichoptera* near the bottom. In fig. 18 the series from the 16th and 23rd of June 1959 represent the vertical distribution of *P. vulgaris* while the series from the 20th of July represent mainly *P. dolichoptera*.

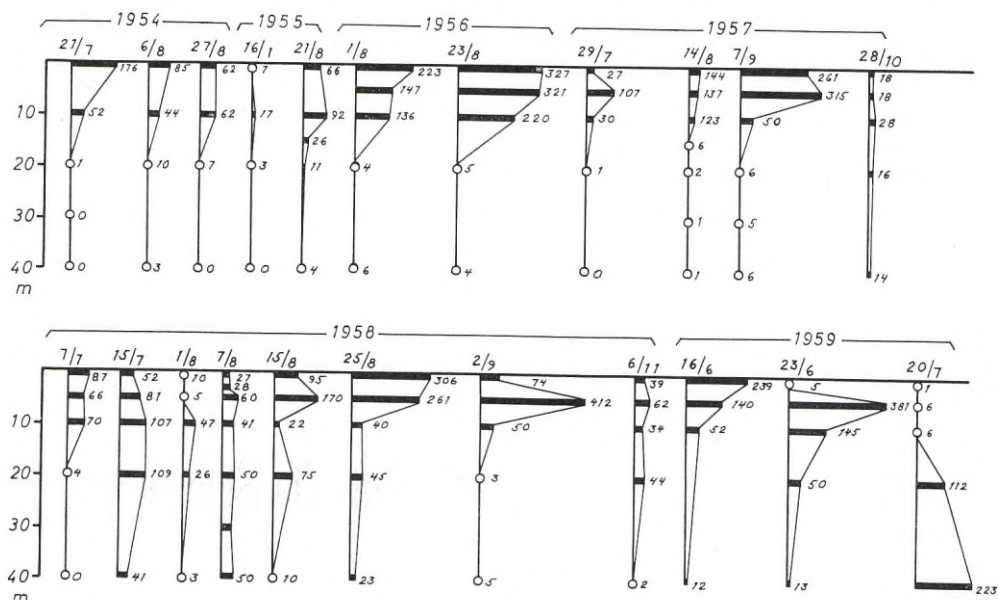


Fig. 18. Vertical distribution of *Polyarthra vulgaris* and *dolichopectera*. (ind./5 l)

Keratella cochlearis (fig. 19). This rotifer seems to prefer the region above and below the thermocline, that is to say the metalimnion. On a few occasions the maximum is developed at the surface but just as often the species avoids these layers.

Kellicottia longispina (fig. 20). This very common rotifer may be considered an epilimnic species though the range into the depths is wider than for instance that of *Polyarthra vulgaris*. Particularly in 1958 high values were obtained in the samples from 20—40 m. I have observed that egg-carrying individuals may be located deeper than the others and I consider this to be due to the increased weight.

Besides the above-mentioned species, diagrams of *Conochilus unicornis*, *Asplanchna priodonta* and *Filinia terminalis* have also been drawn (fig. 21 and 22). Concerning *C. unicornis*, I have already mentioned the difficulty in constructing diagrams of this species. Yet, this rotifer seems to prefer the epilimnic water though it does not avoid the deep layers.

Asplanchna priodonta can also be found in the whole water column. The maxima are sometimes found near the surface and in quite deep water.

Filinia terminalis is a typical cold water form. Maximum is hardly ever observed in the epilimnion, but most often in the samples from 20 m which is often the upper part of the hypolimnion.

Leaving out the cold-stenothermal species of the hypolimnion it may be stated that the plankton animals prefer the layers where the light is abundant enough for a rapid growth of phytoplankton, that is to say to a depth

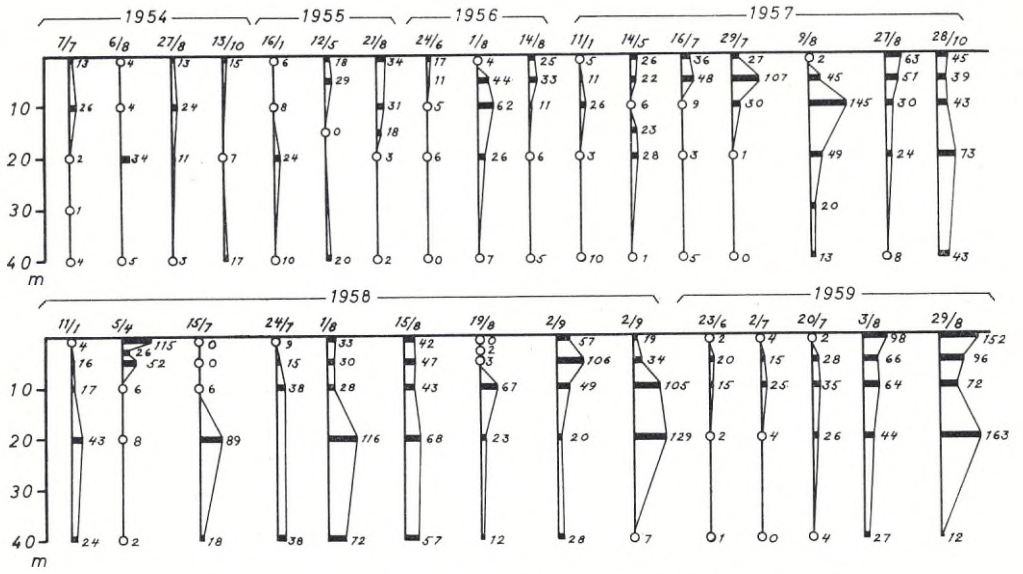


Fig. 19. Vertical distribution of *Keratella cochlearis*. (ind./5 l)

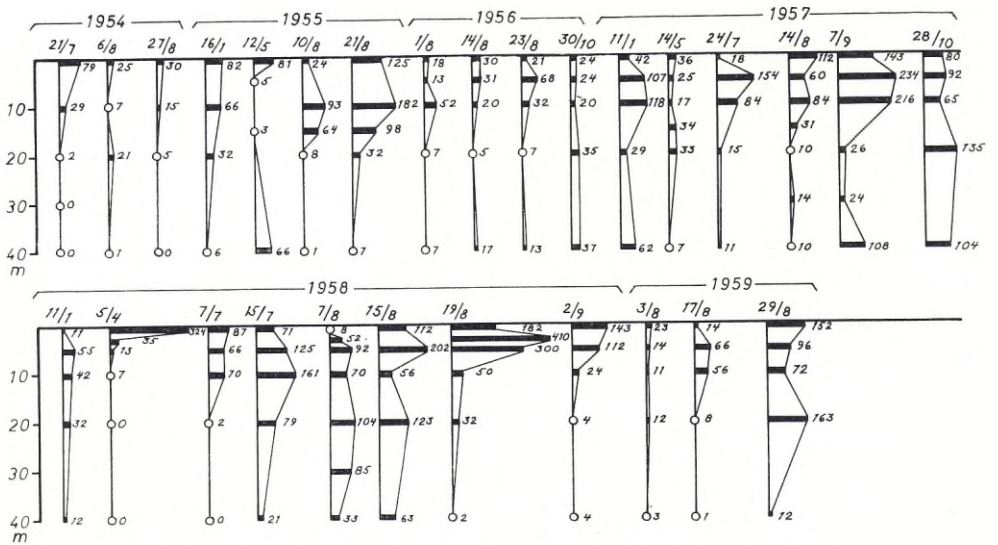


Fig. 20. Vertical distribution of *Kellicottia longispina*. (ind./5 l)

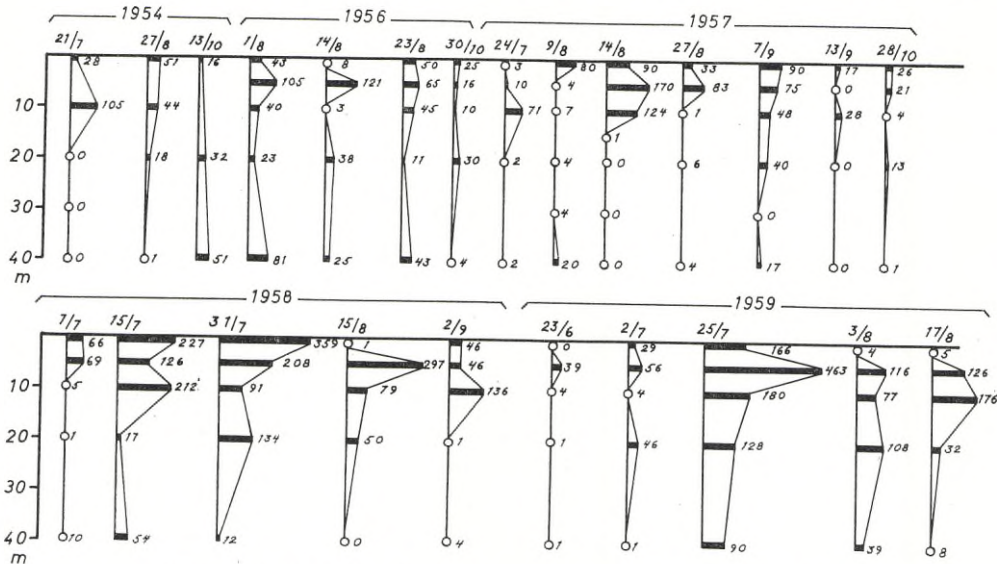


Fig. 21. Vertical distribution of *Conochilus unicornis*. (ind./5 l)

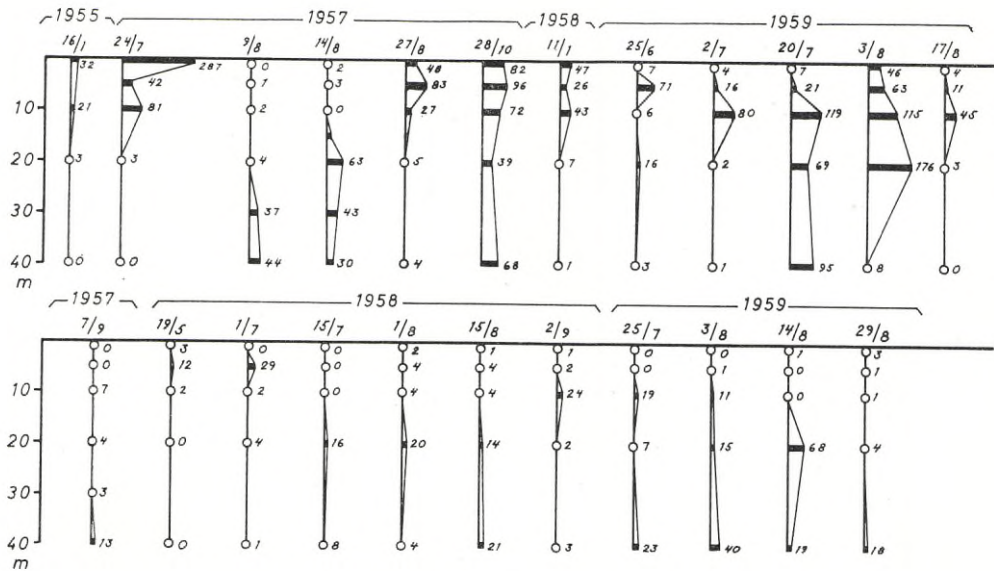


Fig. 22. Vertical distribution of *Asplanchna priodonta* (above) and *Filinia terminalis* (below). (ind./5 l)

of about 10—15 m in Ransaren and Kultsjön. The uppermost layers are avoided by most of the species. This is probably mainly a negative response against light though other factors also may co-operate. Thus the wave action in the surface water may be a barrier against spread into the surface water. NAUWERCK (in manuscript) has found a correlation between the wind force and the vertical distribution of zooplankton in Lake Erken.

Besides the effects of light and temperature the competition for food is probably the dominating factor in controlling the vertical distribution.

In 1958 the highest zooplankton densities ever observed were found in Ransaren. That summer it was also very common to find relatively great numbers of eurythermal species in the deep strata. Though the cause of this distribution is not settled I will propose the theory that these downward movements are due either to an overcrowding in the epilimnion or to improved food conditions in the hypolimnion. Though the productivity of Ransaren was not on a specially high level during 1958 (see chapter VII), an improvement of the food conditions of the zooplankton probably took place in the whole water-body. However, I do not consider improved food conditions to be the only cause for this increase of zooplankters in the hypolimnion. Because of the very inconsiderable outflow from the lake in the summer of 1958 (see further chapter VII) the plankton losses through the outflow were kept on a very low level. It is therefore possible that the epilimnic water happened to contain more animals than could be supported by the food organisms. Together with the competition between the species this meant that the eurythermal species had to extend their distribution to a greater depth than would be the case under normal conditions.

It is noticeable that species ingesting the same kind of food are very often found at the same depth. This is true for *Polyarthra vulgaris* and *Kellicottia longispina*. Both the species ingest mainly nannoplankton of a size below 10 μ (NAUMANN 1923). They may however avoid competing too much by selecting different species of μ -algae. This specialization may also explain why *Polyarthra* and *Kellicottia* are able to develop coincident maxima in their annual cycle. *Keratella cochlearis* and *Conochilus unicornis*, second in order of numerical occurrence, do also ingest food of a size below 10 μ . They are, however, normally not restricted to the epilimnion and *Conochilus* may also, according to NAUMANN, ingest non-living seston.

Concerning the crustaceans it can be said that the adult *Cyclops* is a predator and to some extent also the copepodites. They therefore thrive well in the region where the highest densities of other zooplankters are found. The nauplii feed mostly on nannoplankton, but through their occurrence mainly in the deep strata, they avoid competition from the most common rotifers. *Diaptomus* and *Daphnia* both filtrate small algae of the nannotype and *Daphnia* feeds also on fine detritus and bacteria. Especially *Daphnia* which is sometimes quite numerous in Ransaren in the epilimnion, may therefore be impaired by the competition with the most common rotifers.

VI. The zooplankton of the littoral zone of Ransaren

During the years 1954—1957 only a few samples were taken in the littoral zone of Ransaren. In 1959 the investigation of this zone was more intensive and series were taken along 4 cross-profiles (fig. 23).

In almost every sample from the littoral zone one can notice the small number of rotifers. *Conochilus unicornis* is the most abundant rotifer in the littoral zone, but even this species becomes much more numerous at a distance from the shore. PEJLER (1957) also reports a remarkably poor rotifer plankton in the littoral samples from lakes in Northern Sweden. The crustaceans on the other hand are often very abundant. In Ransaren big swarms of *Diatomus*, *Heterocope*, *Bosmina* and *Polyphemus* have been observed. However, a mass occurrence of all these species at the same time and place has never been seen. A mass development of one species seems almost completely to exclude the others. Some net-samples in 1958 gave the following results. At the northern end of the lake, swarms of *Diatomus laticeps* were found at a depth of about 0.5 m in the beginning of July. In August the littoral zone of the Fabmeluokte Bay was completely dominated by *Polyphemus pediculus*. The examination of char stomachs showed that many fish fed exclusively on *Polyphemus* at that time. In the region of the regulation-dam swarms of *Heterocope saliens* were observed in the beginning of September.

The great numbers of crustaceans that have been observed in the littoral zone of Ransaren, may be a result of the impoundment of the lake, because the submersion of terrestrial areas will improve the environmental condition. However, zooplankton swarms are also found in the littoral of lakes with a normal water level. Great numbers of *Polyphemus pediculus* were found at Saxnäs (Kultsjön) in 1958. As continuous series have not been taken in the littoral zone I cannot judge the regulation effect on the littoral plankton.

In the following I will only deal with the samples from 1959. During all the sampling periods the water level of Ransaren was about 10 m above the mean water level and two of the profiles (C and D) are entirely on the flooded area.

I find it necessary to point out that the following diagrams only give a very crude picture of the plankton distribution. The samples have been taken at some fixed depths and the distance between the deepest stations is quite great. This means that the interpolations between the values will be very uncertain. Bearing this in mind I will only describe the features that seem to be real and the discussion of the diagrams will therefore be very short.

Profile A. (July 11, fig. 24—26.)

Bosmina obtusirostris is very abundant down to a depth of about 10 m. Maximum densities are found close to the bottom. The population density

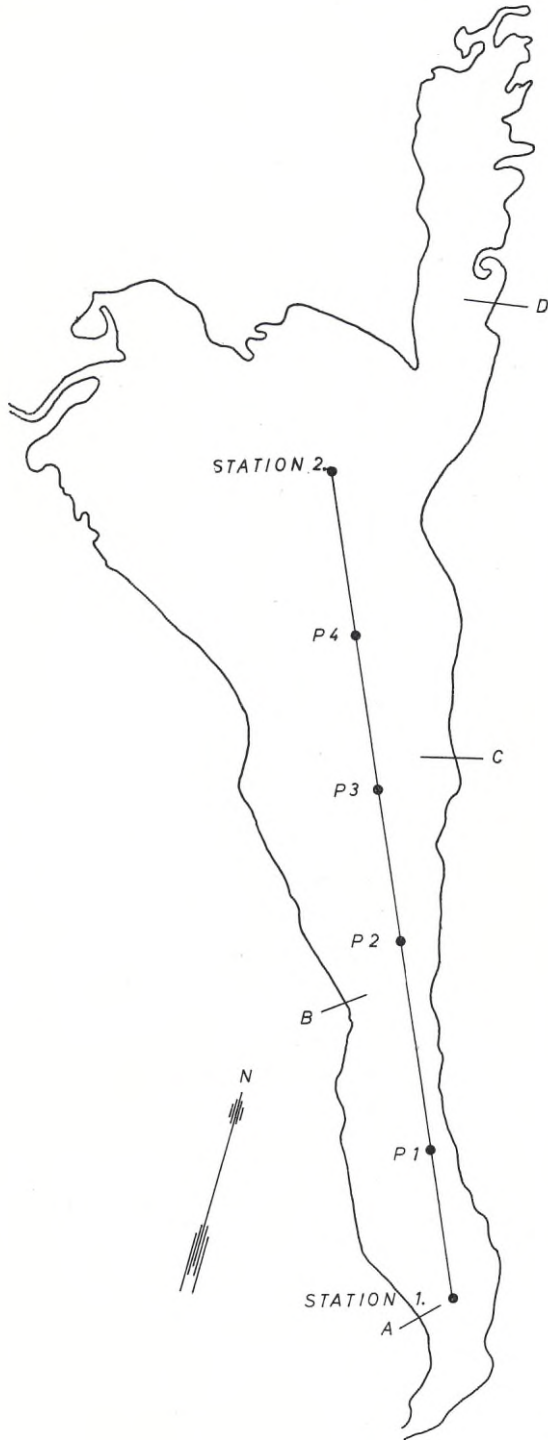


Fig. 23. Zooplankton profiles in Ransaren in 1958—1959.

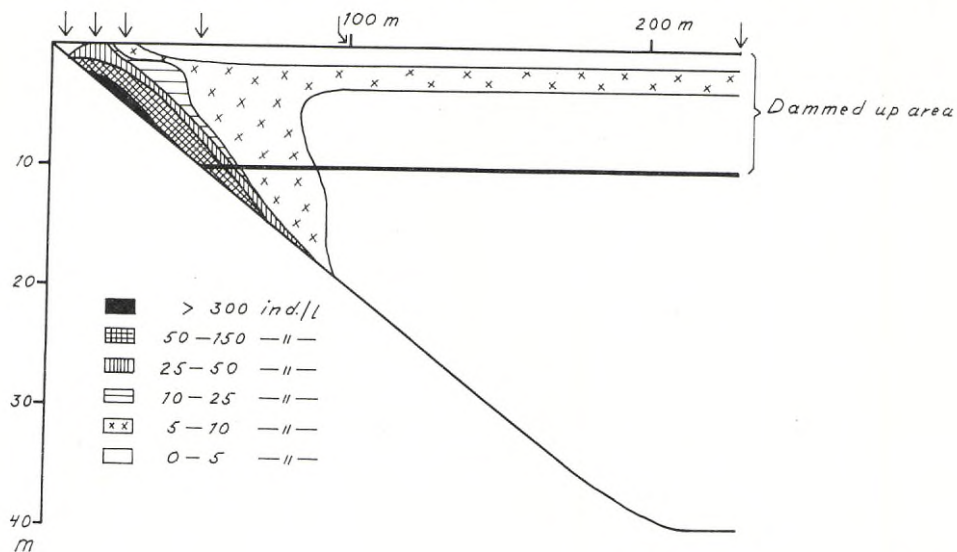


Fig. 24. The distribution of *Bosmina obtusirostris* in the littoral zone of Ransaren (profile A) in 1959.

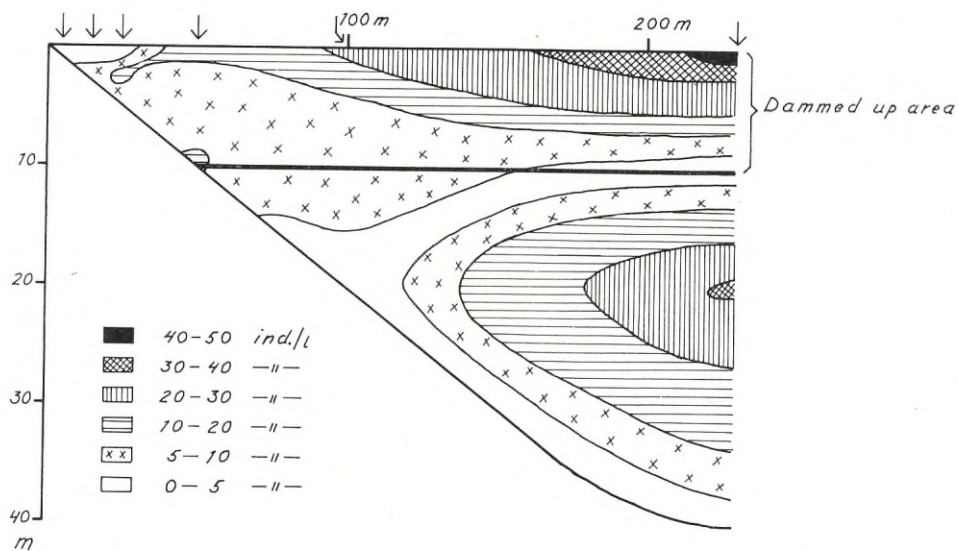


Fig. 25. The distribution of *Conochilus unicornis* in the littoral zone of Ransaren (profile A) in 1959.

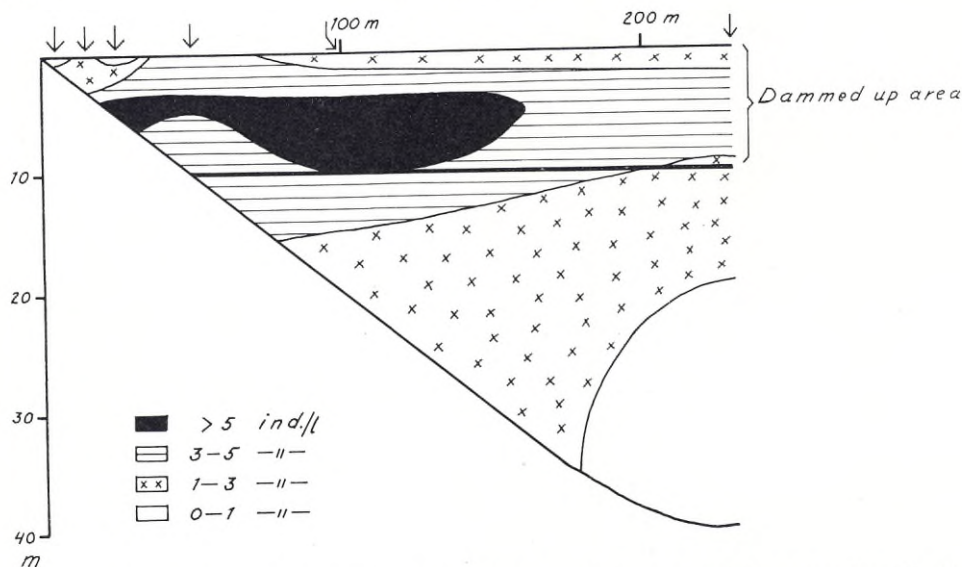


Fig. 26. The distribution of *Keratella cochlearis* in the littoral zone of Ransaren (profile A) in 1959.

decreases rapidly towards the surface. At a depth of 3 m 1680 ind./5 l were found in the bottom water and only 184 at the surface. I have already suggested on page 97 that *B. obtusirostris* is a littoral species which has spread into the pelagical zone in the case of a high population density in the littoral zone. This is confirmed by the cross-profile which shows that at a distance of 100—200 m from the shore the species is found at the 3 m level, a depth at which the greatest number of individuals was found at the shore.

Next to *Bosmina* the rotifer *Conochilus unicornis* is the most abundant zooplankton species in the littoral zone. However, still higher values are found when the depth increases. The tendency in the rotifers to avoid the shallow water is illustrated also by *Conochilus*.

Because of the scarcity of rotifers in the littoral zone as well as low values for many species in the whole lake in the summer of 1959 I have been able to draw only a few diagrams. Besides the above two species a diagram of *Keratella cochlearis* has also been drawn though the numbers of individuals are very few. *Keratella* seems not to avoid the littoral with the exception of a narrow zone close to the shore.

Profile B. (July 16, fig. 27—29.)

The distribution of *Bosmina* is in very good agreement with the conditions at profile A. The high values near the shore and the affinity for the bottom water are very evident. Also in this case there is an off-shore spread at the 3-m level at which depth the highest values of the near-shore water are found.

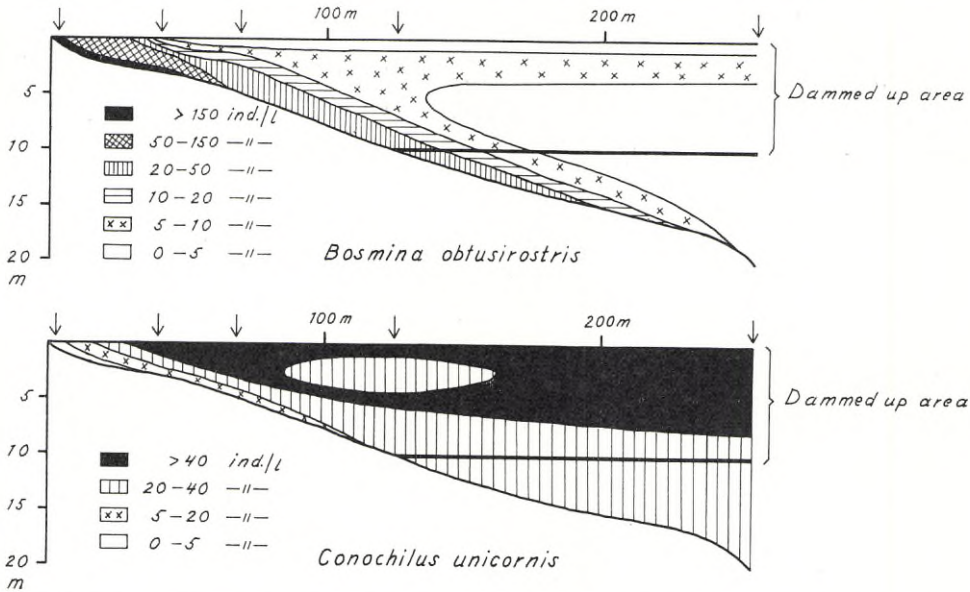


Fig. 27. Distribution of *Bosmina obtusirostris* and *Conochilus unicornis* in the littoral zone (profile B) of Ransaren in 1959.

Conochilus is quite abundant and the picture that is sketched in the discussion of profile A is repeated. Though the species occurs in rather great numbers within the littoral it is still more numerous away from the shore, and the zone close to the shore is quite avoided.

Keratella also avoids the very near-shore water and becomes gradually more numerous at some distance from the shore. The affinity for the surface differs from the vertical distribution that is usually found at a greater depth. I therefore suggest that *Keratella* may develop its maximum closer to the surface in the littoral zone than in the pelagial zone. The avoidance of the bottom water in shallow areas is most probably a result of the mass development of *Bosmina* within this water-mass. This may be true for other rotifers as well.

At this profile the rotifers *Polyarthra* spp., *Asplanchna priodonta*, and *Synchaeta pectinata* were numerous enough to allow the drawing of diagrams. In all the species the typical rotifer distribution is repeated. In shallow water the region of the shore-line as well as the bottom water is avoided. The two maxima of *Synchaeta* in fig. 29 are probably not a true distribution. The maxima ought to be connected with each other. The two *Polyarthra* species have not been separated when counting the quantitative samples. The development of a maximum at a depth of about 20 m indicates that this maximum is caused by *P. dolichoptera*.

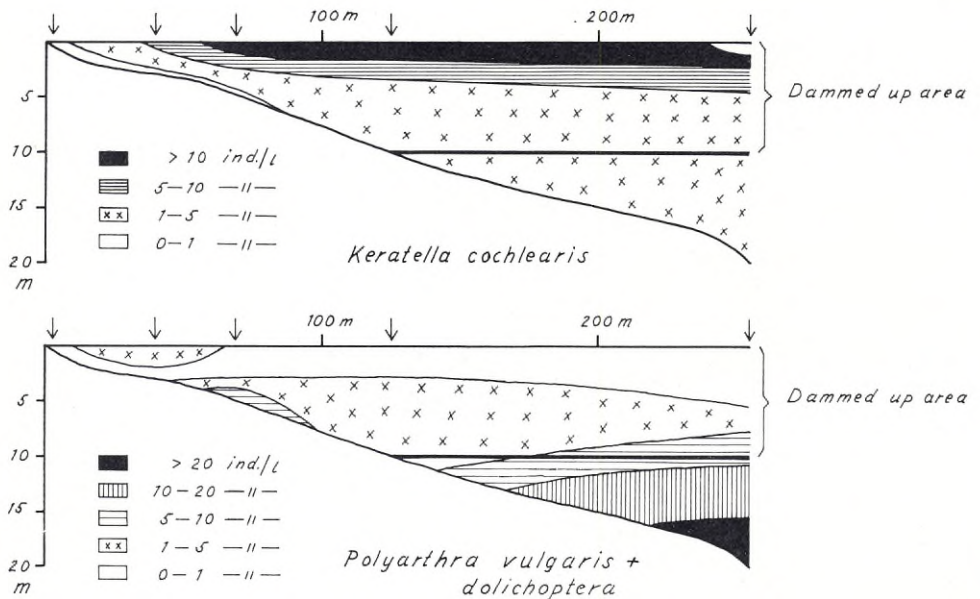


Fig. 28. Distribution of *Keratella cochlearis* and *Polyarthra vulgaris*+*dolichoptera* in the littoral zone of Ransaren (profile B) in 1959.

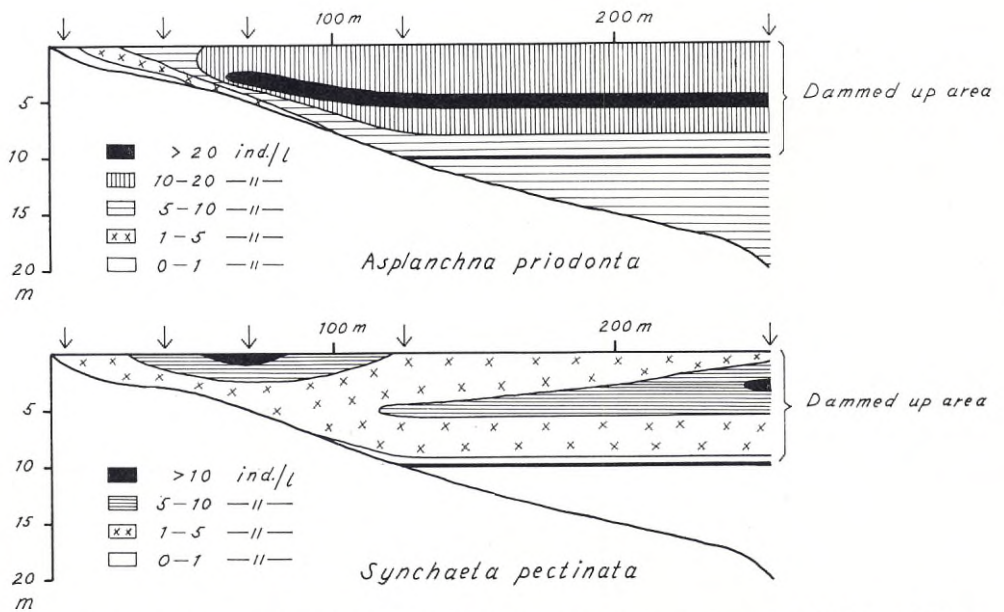


Fig. 29. Distribution of *Asplanchna priodonta* and *Synchaeta pectinata* in the littoral zone of Ransaren (profile B) in 1959.

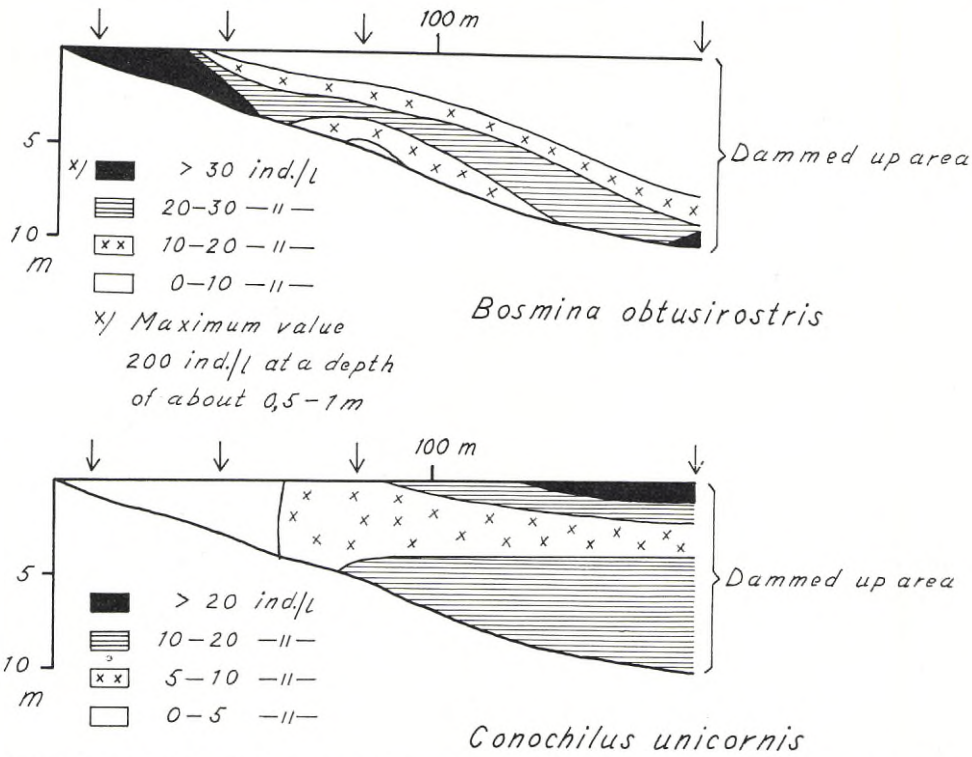


Fig. 30. Distribution of *Bosmina obtusirostris* and *Conochilus unicornis* in the littoral zone of Ransaren (profile C) in 1959.

Profile C. (July 24, fig. 30.)

Samples have only been taken down to a depth of 10 m. This means that the whole profile is over a dammed up area. Only *Bosmina* and *Conochilus* were numerous enough for the construction of diagrams. The distribution of *Bosmina* is the same that has been described above with the highest values near the shore and in the bottom water.

At this profile the *Conochilus* population is quite poor within an area that extends farther from the shore than at the other profiles.

Profile D. (July 24, fig. 31.)

Like the preceding profile this one is lying entirely within the dammed up area of the lake. The results are also the same. Only the values of *Bosmina* and *Conochilus* can be presented in the form of diagrams and the distribution is similar to that of the other profiles with one exception: The maximum of *Conochilus* is not found at the surface but at a depth of about 5 m.

Finally I might add that the wind conditions must also effect the distribu-

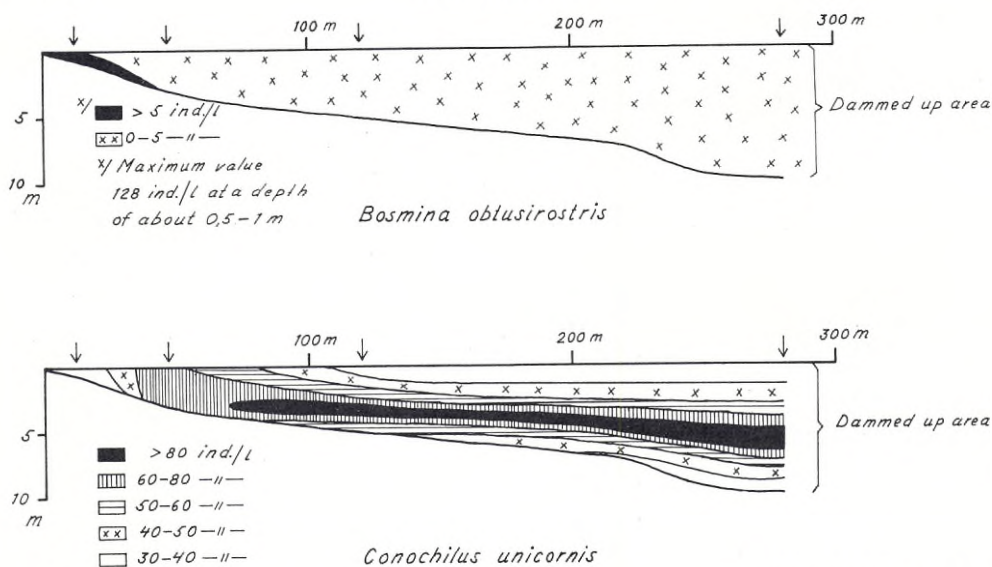


Fig. 31. Distribution of *Bosmina obtusirostris* and *Conochilus unicornis* in the littoral zone of Ransaren (profile D) in 1959.

tion of the littoral zooplankton. Temperature measurements have not been made at the sampling occasions and the effect of the transport of water can therefore not be accurately estimated. However, the good agreement between the profiles indicates that the conclusions that have been drawn from the diagrams are not false.

VII. The yearly variations of the zooplankton with special regard to impoundment conditions

The standing crop of zooplankton in Ransaren passed through considerable changes during the investigation period 1954—1960. Before dealing with the changes combined with the regulation of the lake, I will give a general survey of the yearly development of the zooplankton community in Ransaren. The results are compared with the material from Kultsjön in order to avoid, as far as possible, a confusion of the regulation effects with the natural variation. It is also of the greatest importance to compare the zooplankton values with the results of the phytoplankton investigation. These results are not yet published but some important diagrams have been left at my disposal by RODHE and NAUWERCK (in prep).

The quantitative values in the following diagrams are expressed per surface unit (dm^2). As to the zooplankton values a water column with a height of 40 m has been used, being a representative depth at station 1 in both the

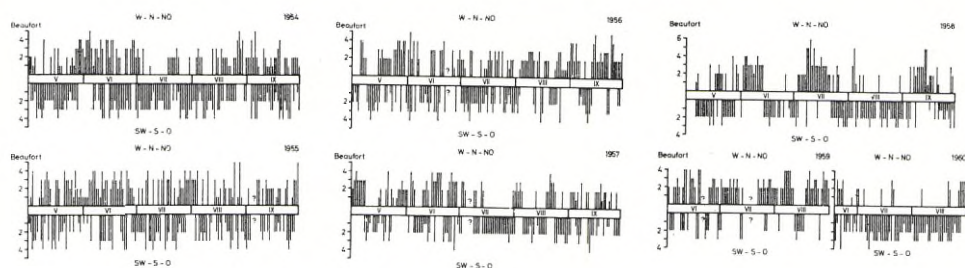


Fig. 32. Wind observations at Klimpfjäll (W. Kultsjön) during the period 1956—1960.

lakes. By multiplying the values with 2.5 the average per m^3 of the whole column is obtained.

As I have pointed out in chapter IV, great variation in the standing crop of zooplankton may occur due to the wind conditions prevailing when the samples were taken. It is therefore necessary to judge the results from this point of view, when dealing with the regulation effects. Doing so, a great source of error can be limited and an overestimation of the results may be avoided. Especially in 1957—1959 such a treatment of the material was essentially necessary because of the great changes in the zooplankton densities that occurred during those years. The results presented below are based on such a control of the values. As to 1958, the year of maximum increase of the species, I have shown in chapter IV that the high values obtained in August at station 1 are by no means too high, but represent a real increase of the standing crop. As a matter of fact there was a loss of plankton due to a surface transport of plankton in a northerly direction. As to the other years, I find it quite unnecessary here to deal with the control of the quantitative values. Suffice it to say that the results have shown that the values presented in the following diagrams may very well be valid for a treatment of the regulation effects. For the sake of completeness the wind observations at the meteorological station at Klimpfjäll (W. Kultsjön) have nevertheless been given in fig. 32.

The yearly variations of the zooplankton

In fig. 33—39 the frequency of some dominant zooplankton species is presented. The copepods *Diaptomus laticeps* and *D. graciloides* are here excluded. As the former occurs in Ransaren and the latter in Kultsjön they can not be used when comparing the lakes in respect to the number of individuals. Later in this chapter, when I deal with the total volume of the zooplankton the *Diaptomus* species must, however, be included because of the great part of the total volume made up by these species.

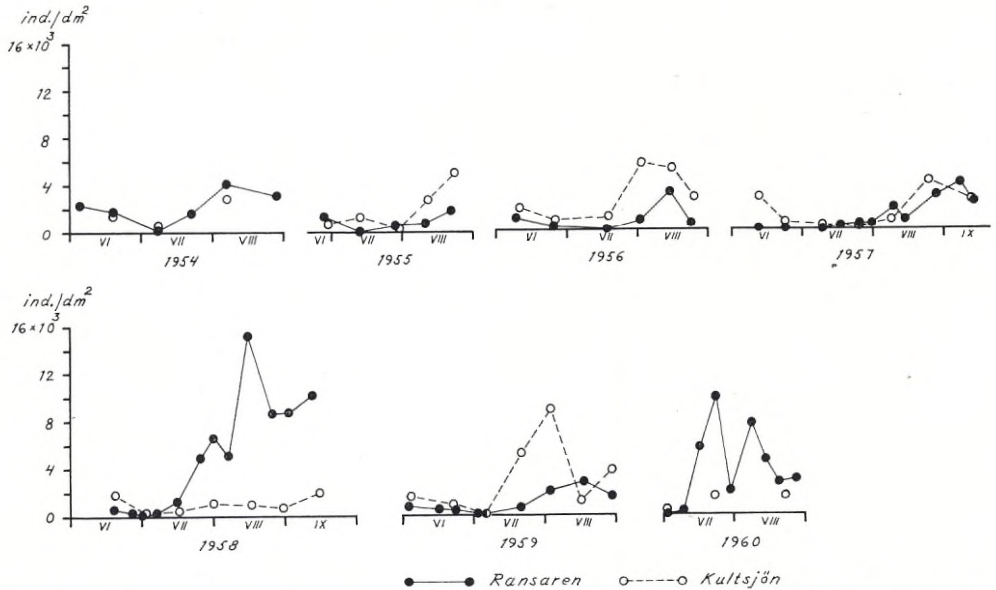


Fig. 33. Variation in nauplii of *Cyclops scutifer* in Ransaren and Kultsjön in the period 1954—1960.

Cyclops scutifer (fig. 33—35)

NAUPLII: In 1954 and 1957 no marked difference between Ransaren and Kultsjön has been observed. In 1955 and 1956 the values from Kultsjön are distinctly higher in August. In 1958 very high values were obtained in Ransaren while there was a decrease in Kultsjön. In 1959 there was a retrogression in Ransaren and a marked increase in Kultsjön. During the last year of the investigation the nauplii values from Kultsjön were rather low, but they were too few to give a reliable picture.

One characteristic feature of the curves is a marked minimum in the beginning of July. The nauplii, before and after this time, originate from different fractions of *Cyclops scutifer* (AXELSON, 1961).

COPEPODITES: There are no distinct differences between the lakes. On some occasions higher values are obtained in Ransaren and on other occasions the relation is the contrary. The highest values were found in 1960 in both the lakes.

ADULTS: The number of individuals varies greatly. During the first years of the investigation period, higher values were found in Kultsjön from June to the beginning of August, while the values from late summer were higher in Ransaren. This difference between the lakes is most probably due to the existence of two different fractions of the species, which develop unequally in the two lakes.

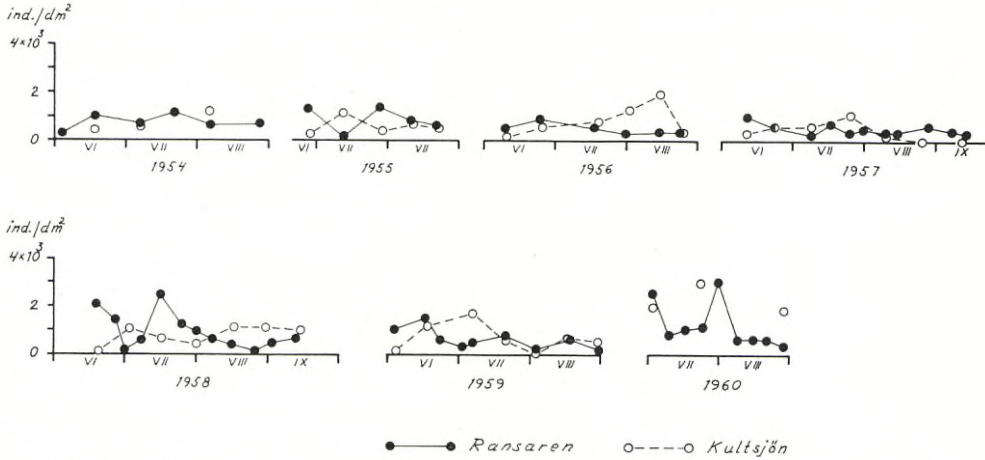


Fig. 34. Variation in copepodites of *Cyclops scutifer* in Ransaren and Kultsjön in the period 1954—1960.

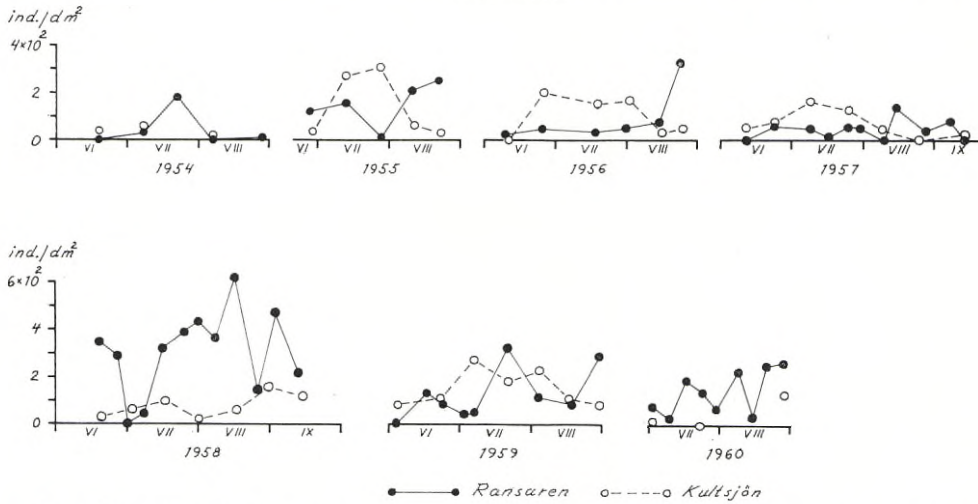


Fig. 35. Variation in the adults of *Cyclops scutifer* in Ransaren and Kultsjön in the period 1954—1960.

In 1958 very high values were obtained in Ransaren compared to the values from Kultsjön, while in 1959 no marked differences were observed in the maximum population level of the lakes.

Daphnia galeata (fig. 36)

In 1954—1956 particularly low values were obtained in both the lakes. In 1957 there was a slight increase and in 1958 the species increased strongly in Ransaren, but remained on a low level in Kultsjön. In 1959 the number of individuals was once more quite low in both the lakes with the exception of one series in Ransaren ix from July 20. Unfortunately the wind observations

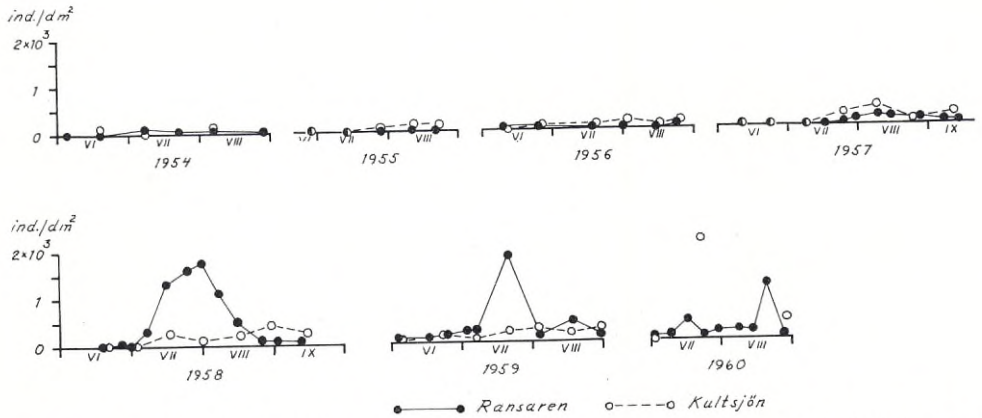


Fig. 36. Variation in *Daphnia galeata* in Ransaren and Kultsjön in the period 1954—1960.

during this part of July give very scanty information, but it seems probable that such a divergence from the general course of the curve represents a value not comparable to the others. It may be a question of a concentration of young individuals in the region of the thermocline.

In 1960 the population is once more quite small in Ransaren. In Kultsjön the same year one series was remarkably rich in *D. galeata*.

Polyarthra vulgaris and *dolichoptera* (fig. 37)

In 1954 and 1955 the curves of both the lakes are kept on quite a low level. In 1956—1959 there is a considerable increase in Ransaren while the popula-

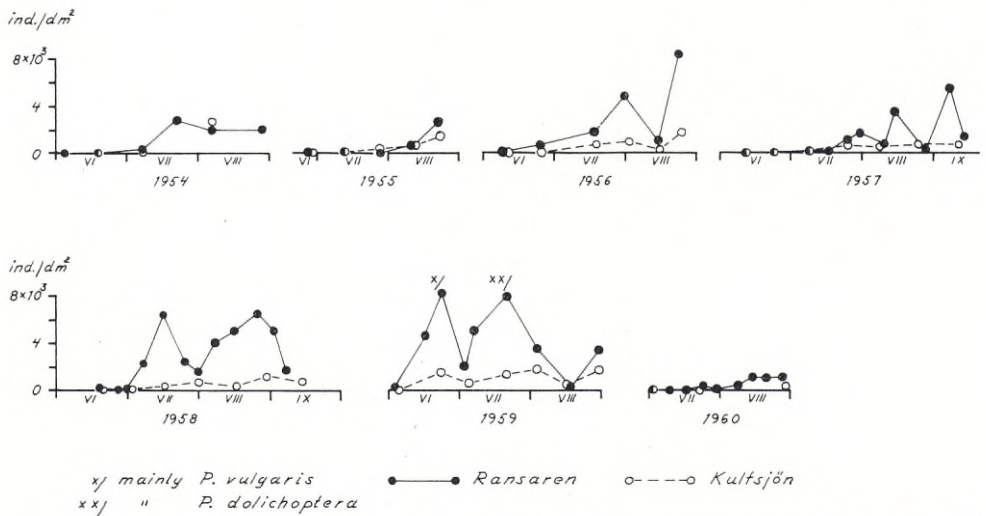


Fig. 37. Variation in *Polyarthra vulgaris* and *dolichoptera* in Ransaren and Kultsjön in the period 1954—1960.

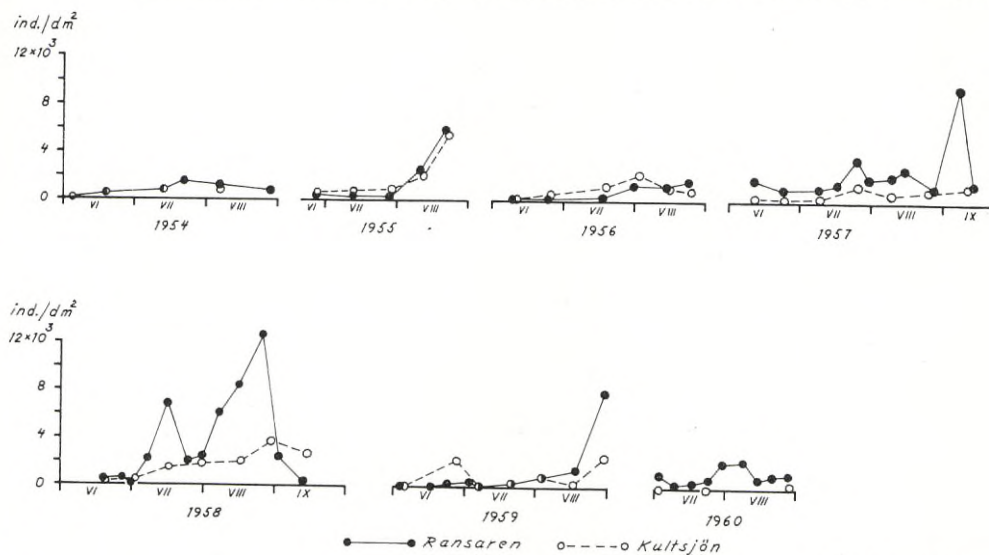


Fig. 38. Variation in *Kellicottia longispina* in Ransaren and Kultsjön in the period 1954—1960.

tion in Kultsjön is still quite few in number. The marked increase of *P. vulgaris* in Ransaren in 1956 indicates that some changes within the lake had taken place already that year. Other rotifers did not show a similar increase and it is therefore possible that *P. vulgaris* is more sensitive to environmental changes than the other rotifers. The interpretation of the results from 1957 is somewhat uncertain as the maximum values in Ransaren originate from samples taken at a time when there was no sampling in Kultsjön. However, the increase of all the dominant rotifers in 1957 and 1958 in Ransaren is general and the recorded values of *Polyarthra vulgaris* in August and September 1957 may therefore be considered a real increase.

In 1959 the June maximum is caused by *P. vulgaris*, which was very abundant in the surface layers, while the maximum in July is due to a rapid growth of *P. dolichoptera* in the bottom water.

The series from 1960 show the lowest values ever observed in both the lakes.

Kellicottia longispina (fig. 38)

In 1954—1956 there was no marked difference between Ransaren and Kultsjön. In 1957 and in 1958 there was a strong increase in Ransaren. The maximum population level of 1958 was obtained when there was a transport of surface water away from the sampling station and I therefore regard this value to represent a real increase. It is most probably too low. The top value of September 1957 on the other hand may be considered a little too high. In 1959 and 1960 *Kellicottia* like many other species is quite few in number. In Kultsjön the number of individuals is kept on about the same level throughout the years.

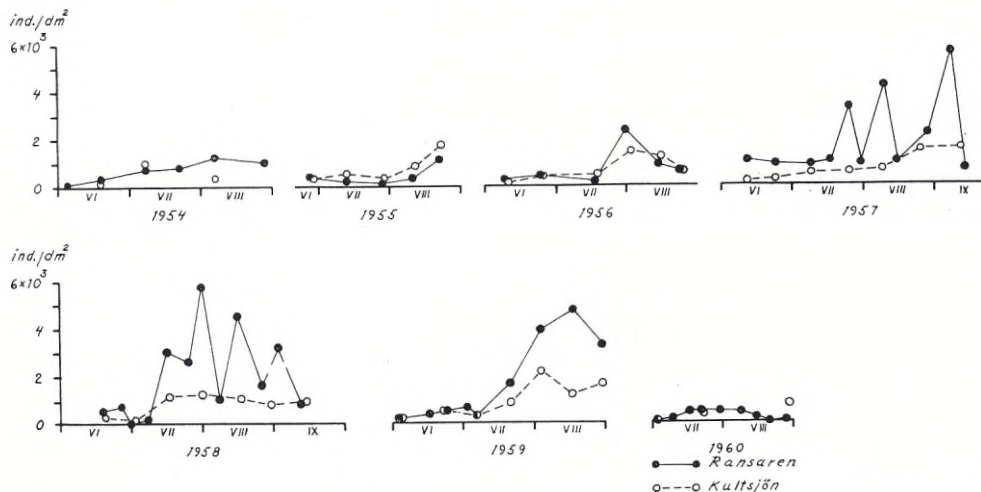


Fig. 39. Variation in *Keratella cochlearis* in Ransaren and Kultsjön in the period 1954—1960.

Keratella cochlearis (fig. 39)

Like the other species there is no marked difference between the lakes during the first years of the investigation. In 1957—1959 there is a considerable increase in Ransaren, while in 1960 low values were found. In Kultsjön no significant changes have been observed.

Summarizing the results described above, it is easily seen that all the important changes in the standing crop of zooplankton took place in Ransaren. The increase in the number of individuals is most clearly visible in 1958 when very high values were obtained for all the dominating species. In 1959 there was a surprising decrease in some of the species. *Kellicottia longispina* and *Polyarthra vulgaris* were remarkably few in number during July and the first half of August, a period during which they normally reach their maximum values. A marked decrease in the number of nauplii of *Cyclops* was also recorded. In 1960 the rotifer population was very sparse.

Above I have described the yearly variations within the species that dominate the zooplankton. This, however, gives a very diffuse picture of the variations of the whole zooplankton community. I have therefore determined the total zooplankton volumes which are presented in fig. 41 (page 147).

In the literature, information of the volume of different zooplankton species is rarely given. Though there is a great need for the publication of zooplankton volumes, most often only the total sum is given. In table 5 I have therefore presented the calculated volumes for the adult specimens of some zooplankton species from Ransaren and Kultsjön. It is necessary to keep in mind that the calculation methods are somewhat uncertain and that the values are only approximate.

Table 5.

	Size variation mm	Average volume mm ³	Calculation method
<i>Cyclops scutifer</i>	1.1 —1.6	$7 \cdot 10^{-2}$	model
<i>Diaptomus laticeps</i>	1.4 —1.8	$14 \cdot 10^{-2}$	"
<i>Diaptomus graciloides</i>	0.9 —1.3	$8 \cdot 10^{-2}$	"
<i>Daphnia galeata</i>	1.5 —2.3	$11 \cdot 10^{-2}$	"
<i>Bosmina obtusirostris</i>	0.7 —0.8	$2 \cdot 10^{-2}$	"
<i>Holopedium gibberum</i>	—	$15 \cdot 10^{-2}$	—
<i>Polyarthra vulgaris</i>	0.10—0.13	$3 \cdot 10^{-4}$	stereometr.
<i>Kellicottia longispina</i>	0.12—0.13	$1 \cdot 10^{-4}$	"
<i>Keratella cochlearis</i>	0.10—0.12	$1 \cdot 10^{-4}$	"

The table above needs in some respects to be explained. Because of the complicated morphology of *Holopedium gibberum* the volume of this species is very difficult to determine. The value in the table is only an estimation that is based on the mean size of the species (excluding the gelatinous sheath) and the volume of *Daphnia galeata*. The values for the size variation of the other species include both males and females and in all species the length of the different kinds of anterior and posterior spines has been excluded. When calculating the total volume it is also necessary to determine the volume for the pre-adult stages. As it is too laborious to separate the growth stages of the crustaceans in every sample and to determine the volume for every stage of all the species, I have in fig. 41 used a mean value for the nauplii and copepodites of the copepods and for the juveniles of the cladocerans.

Beside the total volume in fig. 41 the percentage share of the copepods, the cladocerans, and the rotifers is also given in the same figure. Because of the proposed carnivorous life of the members of the *strenuus* group of the genus *Cyclops* (FRYER 1957), *Cyclops scutifer* and the herbivorous *Diaptomus* species have been separated from each other in the diagram. So far as I am aware of the literature on the subject, there is no information given of the feeding habits of *Cyclops scutifer*. I have tried to analyse some gut contents in the preserved material from Ransaren and Kultsjön. Though the gut contents were almost unidentifiable there were no indications that *Cyclops scutifer* would feed in any other way than the other members of the *strenuus* group.

Beside *Daphnia galeata* the cladocerans are made up of *Bosmina obtusirostris* and *Holopedium gibberum*. The two last species occur too irregularly to allow the construction of separate diagrams, but on some occasions they make up a considerable part of the total volume. As to the rotifers only the dominating species are given. The rotifers make up only a few percent of the total volume and an addition of the less common species can not be reproduced on the diagram.

The general tendency in fig. 41 is the same as described above for the different species. No significant changes in the total volume can be seen in 1954—1957. Then there is a sudden rise in Ransaren in 1958 when very high values are obtained. With the exception of July 20 in 1959, a value which is probably too high (cf. *Daphnia* on page 136), there is a decrease that year, but the volume is on a distinctly higher level than during the period 1954—1957 and such is also the case in 1960.

It may be stated that the total volume of the zooplankton is a function of, inter alia, the capacity of the lake to supply the animals with their food organisms. In other words, the total volume gives some indications of the amount of organic matter that has been transformed into animal tissue. The total volume may, however, remain relatively constant though there are great variations in the composition of the zooplankton. Such was the case in Ransaren in the period 1954—1956 and these variations must be due either to changes in the composition of the phytoplankton or to changes in other environmental conditions which favour some species and inhibit others. Such a favouring or inhibitory factor of the greatest interest is the regulation of Ransaren. When dealing in detail with the variations in the zooplankton of Ransaren it is therefore necessary to pay attention to the primary production and to the standing crop of phytoplankton as well as to the variations in the impoundment conditions.

In Kultsjön the total standing crop of zooplankton has remained practically unchanged through all the years and so has also the composition of the zooplankton community. It may therefore be stated that the changes that have taken place in Ransaren must be due to the regulation of the lake. In the following I will therefore deal mostly with the conditions in Ransaren. It must, however, not be forgotten that the construction of a regulation dam in Kultsjön was started in 1958, but the impoundment is small compared to that of Ransaren and the zooplankton seems not yet to be affected to any considerable extent. There are, however, some values from Kultsjön that need to be explained so I will return to the regulation of Kultsjön in the following.

The impoundment conditions

The literature that deals with impounded lakes gives very scanty information as to the changes of the plankton that are due to the disturbances of the water level in a regulated natural lake. Many reservoirs described are artificial lakes created by the construction of a barrier dam in a river valley. It can also be a question of new water bodies in previously dry areas. A very extensive study of a reservoir of the former type has been performed in the reservoir Sedlice near Zeliv in Czecho-Slovakia (STEPANEK, CHALUPA et al. 1958 and 1959). Though this investigation has given us much important

information from the limnological point of view, the results can not be used to a comparison with the regulation effects in Ransaren. In this and in many other impoundments in Middle Europe the water level is kept on a relatively constant level, while in Ransaren there are great seasonal variations in the water level. SCHRÄDER (1959) has made a comprehensive study of impoundments in Thüringen (Germany) but also in this case the zooplankton results are of very little value when dealing with the conditions in Ransaren. As the reservoirs are to some extent polluted by industrial wastes, SCHRÄDER gives his main attention to the Saprobien system. Other papers deal with fishery problems and only a few notes on the plankton are given. RAWSON (1958) and CUERRIER (1954) consider the plankton changes to be quite small in some North American reservoirs. The qualitative and quantitative composition of the standing crop of plankton was almost the same before and after the regulation in these waters. A small increase after the regulation was, however, recorded.

In Norway, DAHL (1926 and 1933) and HUITFELDT-KAAS (1935) have investigated regulated lakes of the same kind as Ransaren. They have given basic information of the regulation effects on the fish and their food organisms. Beside fishery problems they deal mostly with the bottom fauna, including strictly littoral cladocerans, and their results are therefore more useful for the fishery biologists than for the investigator of the pelagical zooplankton.

Though regulated lakes in Northern Sweden have been carefully investigated from the fishery point of view, quantitative records of the zooplankton are entirely lacking. I therefore hope that the present investigation will fill a gap in our present knowledge of regulation effects in North Swedish lakes.

The regulation of North Swedish lakes usually implies a filling of the reservoir in spring, summer, and autumn and a drawing off of water in winter. The raising and lowering of the water level is often of a considerable amplitude, being 18 m in Ransaren, 12 m above and 6 m below the old mean water level. Such a disturbance of the water level has left its mark on the shores, but the erosion has been quite moderate. From other lakes in Northern Sweden it has been reported that the great variations of the water level may be a catastrophe for the bottom fauna. Thus GRIMÅS (1959) has recorded a loss of 70 % in Lake Blåsjön. As the bottom organisms make up the most important source of food for the trout and the char, the impoverishment of the bottom fauna seriously affects the fish population (RUNNSTRÖM, 1955 and NILSSON, 1959). During the first years of a regulation, the decrease of the bottom fauna may be compensated by the addition of food (i.e. drowned insects) due to the flooding of terrestrial areas. Without giving any quantitative data the same authors point out that there seems to be a considerable increase in the littoral cladocerans in the beginning of a regulation, *Eurycerus lamellatus* often being the dominant species. When the

bottom organisms decrease in number and the competition for that kind of food becomes too strong, the char particularly may switch to a plankton diet, thus utilizing the increasing standing crop of littoral cladocerans (NILSSON 1955). Due to the addition of new food supplies in the first years of a regulation, an increased growth of the fishes is often observed. This beneficial effect of the regulation is, however, of short duration and after some years a marked decrease in the size of the fish is to be expected (RUNNSTRÖM *op. cit.*).

Beside the addition of living or dead organic matter from the flooded areas, the raising and lowering of the water level will also add a considerable amount of inorganic nutrients to the lake. This can be caused either by the soaking of terrestrial areas at high water or by the aeration and ice-erosion of bottom sediments at low water. The chemical data from Ransaren (LINDGREN *in prep.*) indicate that only slight changes have taken place in the water chemistry. The plankton investigations give a more distinct picture of the fertilizing effect of the impoundment. This discrepancy between the actual effects of the addition of nutrients and the results of the chemical analyses is easily explained. In an oligotrophic lake the primary production is limited by the available amount of nutrients, nitrogen and phosphorus being the most important. Within moderate limits any addition of these limiting nutrients will immediately be assimilated by the algae, which results in an increased primary production, and on many occasions almost undetectable amounts of $\text{NO}_3\text{-N}$ and $\text{PO}_4\text{-P}$ thus remain in the water. On other occasions Lindgren (*op. cit.*) has observed relatively high values of phosphorus and nitrogen in both Ransaren and Kultsjön. In Ransaren the increase is ascribed to the draw off of water in winter, the ice-erosion thus adding a considerable amount of nutrients to the lake. Lindgren considers the increase in Kultsjön to be due to either the construction of the dam at the outflow from the eastern basin or to the clearance of the shores and burning of the cleared vegetation when preparing the basin for the coming regulation. Particularly the latter explanation seems very reasonable to me. In rainy weather or at a high water level the ash may be washed into the lake and spread within the surface layers, which also explains some recorded surface maxima.

The rate of flow through a lake is another very important factor in controlling the plankton densities in an impounded lake. In a previous paper (AXELSON 1957) I have already touched upon this problem and before passing over to a more penetrating description of the changes in the zooplankton it is necessary to deal with the recorded variations in the discharge and the ways in which the plankton may be affected.

RUTTNER (1930) considers the flow of water through a mountain lake to be of the greatest importance in removing plankton from the lake. He supposes that the crustaceans may to some extent withstand the draw, while

the rotifers and all the phytoplankters may be considerably affected. BROOK and WOODWARD (1956) have made a special study of the influence of the outflow of water in some Scottish lochs. Knowing the volume and the discharge from the lakes, they have determined the replacement times for the water and they have found the flow of water through the lochs to be of fundamental importance in producing quantitative and qualitative differences in the plankton of lakes with high rates of water replacement. BROOK and WOODWARD have also made some special observations on the effectiveness of some crustaceans to avoid the outflow. They have shown that the success in evading the outflow increases with age, but that senile adults can not withstand the draw. As to the phytoplankton they give a valuable piece of information that the only species that may succeed in lochs with short replacement times are those which reproduce rapidly and which possess low nutritional requirements. EINSELE (1960) has also paid attention to the losses of plankton that can be caused by a high rate of discharge. He points out that a very rapid flow of water through a lake involves a "biological catastrophe". RAWSON (1958) has studied impounded lakes in North America and is also aware of the impoverishing effect of a sudden increase in the rate of discharge.

In the impounded lakes of Northern Sweden the filling of the reservoirs during the ice-free season implies that the rate of discharge is often extremely low during the growth period. It is therefore very reasonable to suppose that there may be an increase of the whole standing crop of plankton due to reduced losses through the outflow. The draw off of water in winter does not appear to affect the zooplankton to any considerable extent. The numbers of individuals in winter are very small and the species then prefer the deeper layers or hibernate with resting eggs on the bottom mud.

In an undisturbed lake the highest rate of discharge occurs during the melting of the snow in spring and during rainy periods in summer and autumn. Usually, however, a high rate of discharge seldom takes place during the most important growth period, and though there may be a considerable loss of plankton even under "normal" conditions, a much greater effect is to be expected in the case of a sudden draw in summer from the regulated lake.

From the discussion above it can be stated that there are two important ways in which the variations in the rate of discharge from a regulated lake may affect the zooplankton community:

1. A decrease of the zooplankton due to sudden or unusually high rates of discharge during the growth period, July and August being the most important months in Ransaren.
2. An increase of the zooplankton due to almost a complete closing of the reservoir during the whole ice-free season. The lowering of the lake in winter does not affect the zooplankton to any greater extent.

As to statement 1 it is to be supposed that the effect of a draw is not restricted to the year when it happens. A removal of zooplankton during one summer implies that a fewer number of individuals or resting eggs has been left to pass the winter than would have been the case if the draw had not taken place.

In fig. 40 the variations in the water level and in the discharge of Ransaren are given. In order to facilitate the reading of the following discussion I will give a summarizing survey of the regulation conditions during the years considered here.

1954

The construction of the dam was started and the shores were cleared of all the vegetation above a certain maximum size. The water level varied around the natural mean value (24 m on the diagram) and the discharge was also that of an undisturbed lake with top values in spring and early summer and some small maxima in summer and autumn. Though the construction of the dam and the clearance of the shores to some extent may have affected the metabolism of the lake, the zooplankton values from 1954 may be considered to represent the conditions of the undisturbed lake.

1955

In winter the lake level was lowered down to the lower limit of the regulation (18 m). In the beginning of the ice-free season there was a damming of the lake and a water level of 25 m was reached. Because of the floating of timber a considerable amount of water was drawn off particularly during July, the mean discharge being 73 m³/sec. Due to the down-flow of water at the outflow it may be supposed that mostly epilimnic water was lost through the outlet. Calculating with an epilimnion of about 10 m thickness, which is very often the case in Ransaren, the replacement time, volume of the epilimnion/discharge per day, will be 31 days. Such a rapid exchange of water must affect the plankton and I will return to this in the following pages. In the end of August and in September the discharge was low and the water level slowly rose.

1956

In winter the lake was lowered to the 18 m level. The biggest draw from the lake occurred in June. During July, August, and September the rate of flow from the lake was very small and the impoundment resulted in a raising of the water level to about 27 m.

1957

The first year of almost full impoundment. The discharge varied between 2 and 5 m³/sec and a water level of about 35 m was reached, that is to say only 1 m below the upper limit for the impoundment.

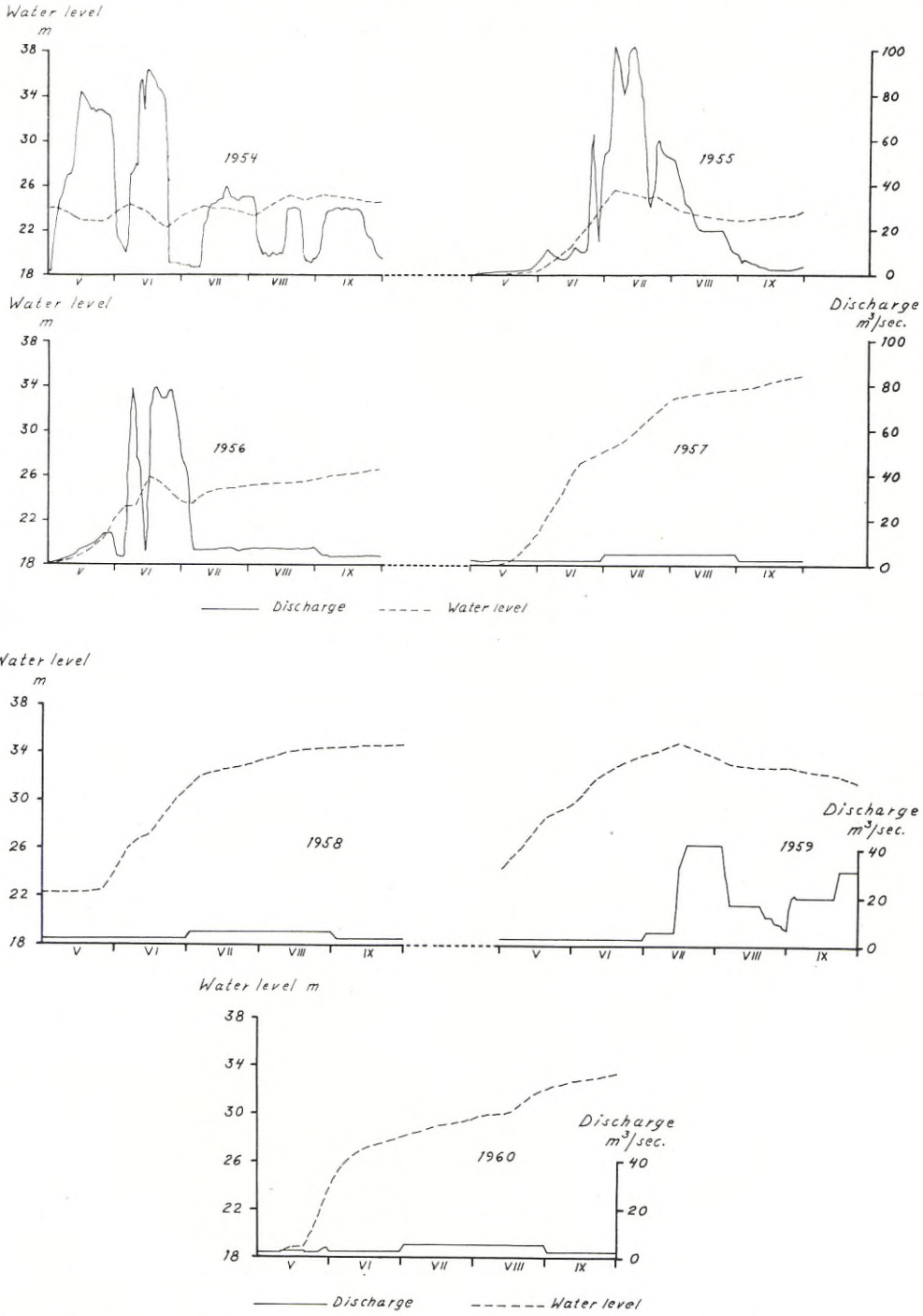


Fig. 40. Water level and discharge in Ransaren during the period 1954—1960. Water level according to the local meter system.

1958

After the draw in winter the level of the lake was on about 22 m. The last 4 m within the regulation zone were thus not utilized. As in 1957 the discharge in summer was extremely low and a water level of 34 m was reached.

1959

The lake was only lowered to a level of 24 m, 6 m thus remaining to the lower limit. During the period from April to the middle of July the discharge was only 2—5 m³/sec, and the water level reached a value of 34,8 m. Due to a repairing of the barrier dam in the northern end of Ransaren it then became necessary to lower the water level. During the period July 14—August 14 the mean discharge was 34 m³/sec and the water level was lowered about 2 m. Calculating with a water level of about 34 m (10 m above mean water) the volume of the epilimnion will be about $270 \cdot 10^6$ m³, and the calculation of the replacement time gives a value of about 104 days. This means that in the above-mentioned period about 30 % of the epilimnion was flowing out through the outlet.

1960

The impoundment of 1960 corresponds to that of 1957 and 1958. The discharge was very low during summer and a high water level was reached. The filling of the reservoir was slightly slower than in 1957 and 1958. In 1960 the lake was lowered to the lowest permissible level (18 m), thus differing from the conditions in the preceding two years.

As I have pointed out above the construction of a regulation dam in Kultsjön was started in the summer of 1958. In the summer of 1960 the works were not yet finished, but a partial regulation took place during the building time. Compared to Ransaren a full regulation of Kultsjön is quite small, being 2 m above and 4 m below mean water. The first draw of water took place during the winter of 1958—1959 when the level of the lake was lowered 4 m. In the summer of 1959 there was a small impoundment. During the rainy summer of 1960 the upper limit for the regulation was reached and on a few occasions even passed.

Discussion

In the period 1954—1956 the impoundment of Ransaren was quite considerable. The primary production (fig. 42) increased slightly in 1955 and in 1956 rather high values were obtained. As a simultaneous increase was also recorded from Kultsjön, the climatic conditions were most probably the decisive factor (RODHE 1957). NAUWERCK (1957) reports, however, an effect of the building of the dam in Ransaren. He considers the remarkably great number of diatoms, mainly *Asterionella formosa*, in the summer of 1954 to be due to an addition of nutrients from the area of the dam. As the ordinary

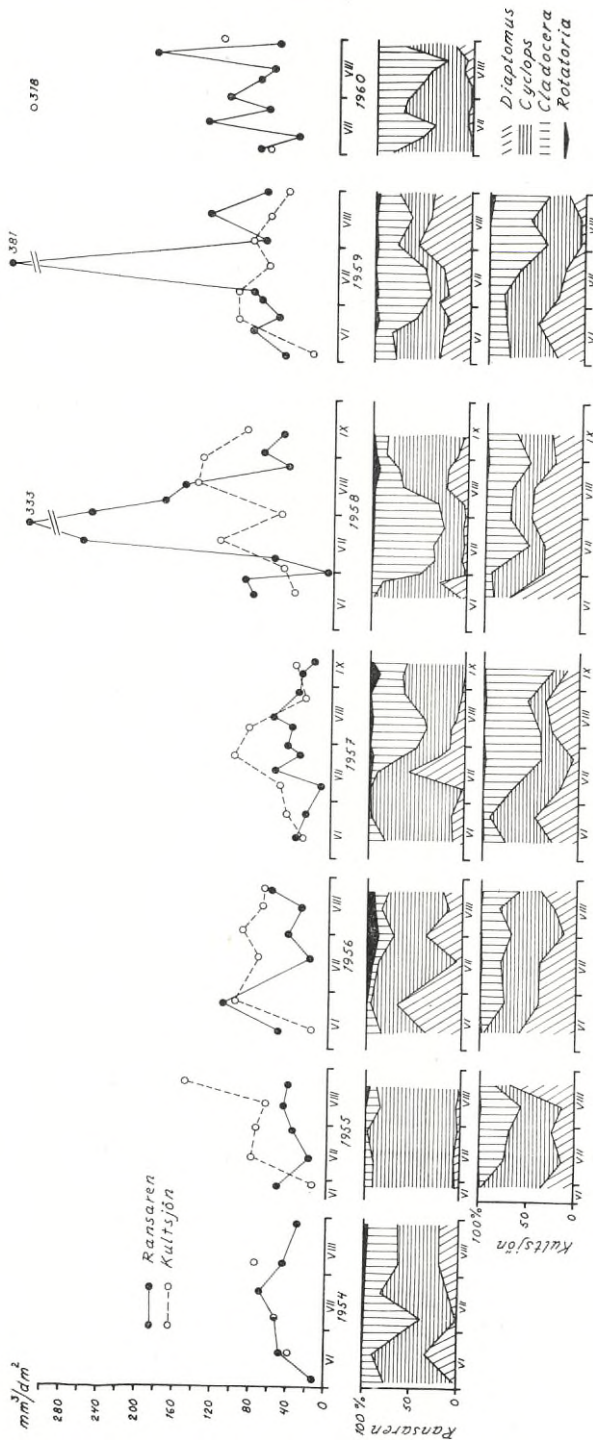


Fig. 41. Variation in the total volume and the composition of the zooplankton in Ransaren and Kultsjön in the period 1954—1960.

sampling station in Ransaren is situated quite near the dam, it is very likely that such is the case. It must, however, be pointed out that even in this case the burning of cleared vegetation on the shores may be responsible for a considerable part of the increase.

Compared to 1954 the volumetric composition of the zooplankton (fig. 41) has markedly changed in 1955. This year, *Cyclops scutifer* makes up about 80 % of the total volume, while the cladocerans and *Diatomus laticeps* are of less importance. As the carnivorous *Cyclops scutifer* may feed upon *Diatomus*, the population of the latter species may suffer from the predation by *Cyclops*. However, the numbers of *Cyclops scutifer* in the predatory stages are not markedly higher in 1955 and it therefore remains to explain why *Diatomus* could not hold its position that year. FRYER (1954) has found that *D. laticeps* may feed exclusively on the diatom *Melosira italica* in Lake Windermere. If such a specialization also occurs in Ransaren, the decreased importance of *D. laticeps* in 1955 may be due to variations in the number of food organisms. This, however, can not be settled. NAUWERCK (op. cit.) gives the sum of the *Melosira* species, but the recorded yearly variations of the species do not show any significant relationship to the variations of *Diatomus laticeps*.

On page 144 I have suggested that the mean draw of 73 m³/sec in July 1955 must have affected the plankton of Ransaren. As to the rotifer population, there is a marked delay in the development in July and the mean value for the standing crop of algae (fig. 43) is also rather low this year. On the basis of the proposed effect of the draw, the changes in the composition of the zooplankton may be explained. *Cyclops scutifer*, feeding mainly on *Diatomus*, holds its position while *Diatomus*, as well as the cladocerans and the rotifers, suffers from the decreased supply of food that is due to the losses through the outflow. As to the rotifers they are as well themselves to a great extent hit by the draw.

The zooplankton picture from 1954 is to some extent reestablished in 1956. *Diatomus laticeps* makes up quite a considerable part of the zooplankton volume and even the rotifers are of increased importance. As the highest rate of discharge occurred in June it did not affect the zooplankton to the same extent as in 1955.

In 1957 the maximum values for the primary production were distinctly higher than in the preceding years while the mean value (fig. 44) was on the same level as in 1956. The standing crop of phytoplankton did not differ significantly from the values of 1956 and that was also the case for the total volume of the zooplankton. It is interesting to find that this first year of almost full impoundment did not affect the productivity of the lake.

Concerning the zooplankton, the cladocerans increased a little and so also did the rotifers at the end of the summer. I consider this increase to be due to reduced losses through the outflow. An increase of the zooplankton due



Fig. 42. Variation in the primary production in Ransaren and Kultsjön in the period 1954—1959. (After Rodhe.)

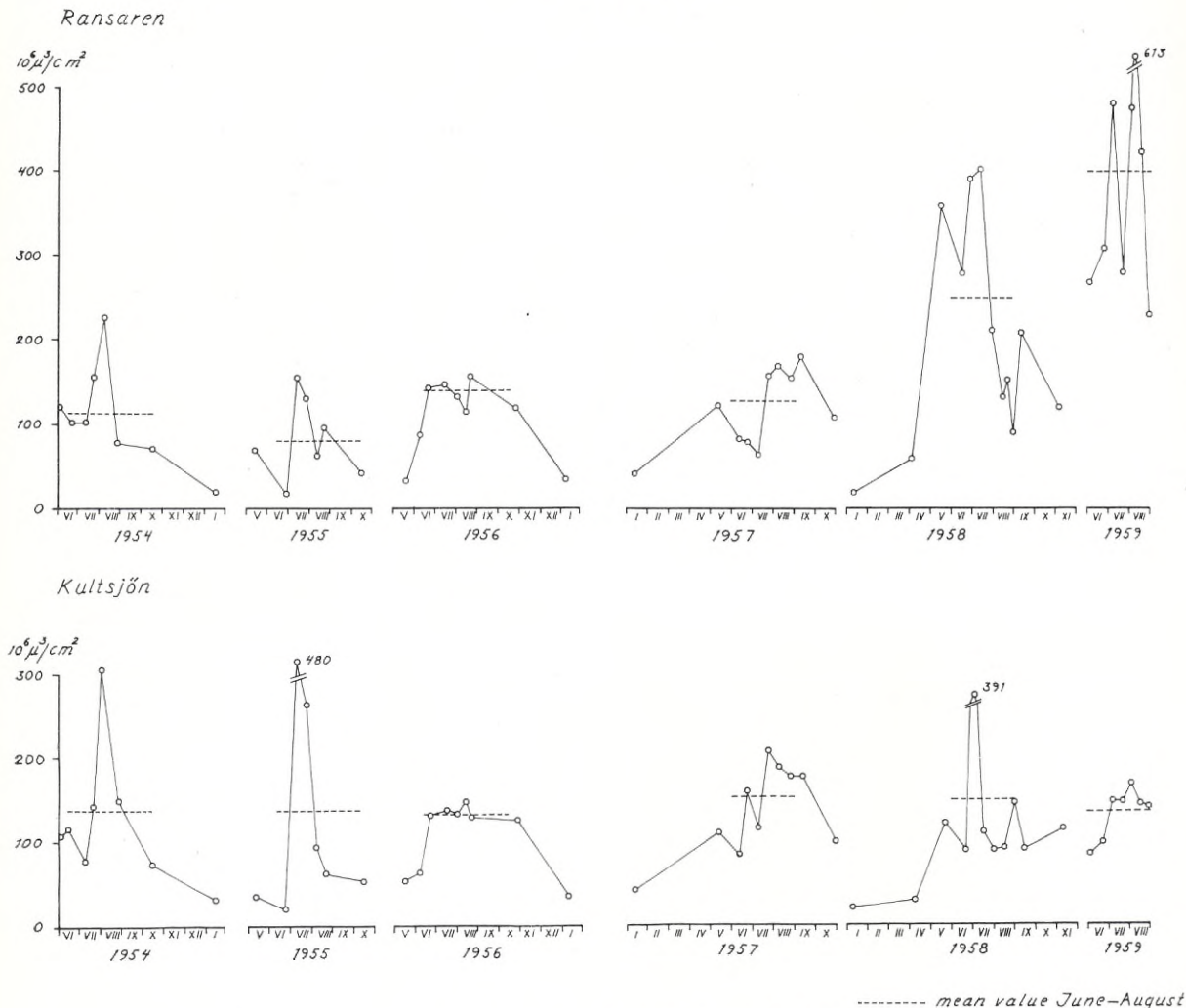


Fig. 43. Variation in the standing crop of phytoplankton in the layers between 0—10 m in Ransaren and Kultsjön in the period 1954—1959. (After Nauwerck.)

to a retention of individuals that otherwise would have been carried away from the lake is still more accentuated in 1958. This creates an ecological problem of the greatest interest.

In 1958 the primary production was lower than in the preceding two years. Yet, both the standing crop of algae and the zooplankton increases to a considerable extent. With the exception of a few species, which show a marked periodicity, the increment of the zooplankton is true for all the species. The problem now is: How is it possible that the recorded relatively low primary production can support such a large standing crop of zoo-

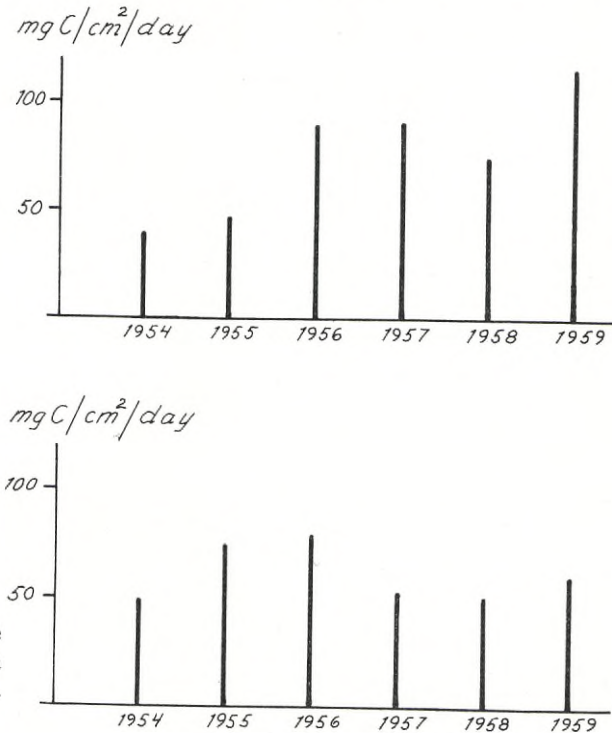


Fig. 44. Summer means for the primary production in Ransaren (above) and Kultsjön (below). (After Rodhe.)

plankton and why is not the grazing of the numerous zooplankters reflected in the standing crop of algae?

As in 1957 the draw off of water in summer was extremely low in 1958. Because of the low discharge in 1957 it may be assumed that the number of resting eggs and individuals that pass the winter is unusually high. In 1958 another summer of full impoundment follows and very high zooplankton values may be expected. The lake will thus contain a great number of animals that in a "normal" lake would have been lost through the outflow. This may cause an increased competition and a lack of food. In chapter V, I have shown that in the summer of 1958 most zooplankton species occur in deeper layers than they ordinarily do. I also proposed a theory that this spread into the deep strata was due to an increased competition in the epilimnion. The species would thus be able to avoid too strong a competition by extending their distribution to involve the whole water body. Yet, as a matter of fact, at the time for maximum abundance many individuals seemed to be in a very bad condition which is exemplified by the values observed at station 2 in the beginning of August. They show a very rapid decrease following the maximum of *Polyarthra vulgaris*, *Kellicottia longispina* and *Daphnia galeata* (cf. chapter IV).

It remains, however, to explain how the phytoplankton can remain on

a high level while, at the same time, there is a lack of food for the zooplankton. It is possible that the reduced rate of discharge to some extent causes the increase of the phytoplankton and that simultaneously the composition of the algae is changed. They may from the volumetric point of view be dominated by species that are not suitable as food for the zooplankton. The chrysomonads, for instance, which include many important "food species" are quite few at the time for some of the maxima on the curve in fig. 43 (NAUWERCK in prep.).

There may, however, be another explanation. In 1958 a dominating part of the zooplankton volume is made up of the cladocerans, particularly *Daphnia galeata*. An increased importance of the cladocerans was observed even in 1957 and relatively high values were also recorded in 1959 and 1960. According to NAUMANN (1921) and NAUWERCK (1959) *Daphnia* filters without any choice for special food organisms. Beside nannoplankton bacteria and fine detritus may thus also constitute a considerable source of food for *Daphnia*, and this may also be true for the other filtering cladocerans. Due to the almost complete closing of the lake in the summer of 1958 the reduced losses through the outflow also involved more or less decomposed organic material. It is therefore very possible that there existed in Ransaren a considerable amount of bacteria and detritus and that this kind of food was utilized to a great extent by the filtering zooplankton species. The above recorded anomaly between the production and the standing crop of algae on one hand and the zooplankton on the other can thus be quite reasonably explained.

During the period of a high discharge in Ransaren in 1959 the epilimnic rotifers *Polyarthra vulgaris* and *Kellicottia longispina* were remarkably few in number and so also were the nauplii of *Cyclops scutifer*. With the exception of one top value on July 20, and this is most probably too high, there is a small decrease also of *Daphnia galeata* and adult *Cyclops*. The total volume of the zooplankton is also markedly lower in 1959 than 1958 with the exception of the mentioned top value of July 20.

The decrease of many zooplankton species in the summer of 1959 thus provides a further evidence for the opinion that the discharge from Ransaren is of the greatest importance in controlling the zooplankton development. According to BROOK and WOODWARD (op. cit.) and the results from Ransaren in 1955, the draw of water does not only affect the plankton quantitatively but there is also a change in the composition of the plankton. This is further illustrated by the findings in 1959. It may be supposed that due to the high production of the phytoplankton and the decreased number of zooplankton in the epilimnion, there was an increase of food sinking down into the hypolimnion. *Keratella cochlearis*, for instance, may have been favoured by the increased supply of food, and increased rapidly parallel with the decrease of *Polyarthra vulgaris* and *Kellicottia longispina*. In 1959

high values of *Keratella* were observed in the epilimnion though the species shows a preference for the layers of the thermocline. *Keratella cochlearis* may however not be considered strictly a hypolimnetic species and under the prevailing conditions of July and August 1959 a spread towards the surface may have taken place. Another example is provided by *Polyarthra dolichoptera*. During the period of a high discharge from the epilimnion the decrease of *P. vulgaris* was followed by a corresponding increase of *P. dolichoptera* in the bottom water.

Even the nauplii of *Cyclops* must have been favoured by the improved food conditions in the hypolimnion, but yet they are quite few in number. However, the number of nauplii are depending on the number of eggs that are hatched and as the eggs are delivered by the preponderantly epilimnetic females the standing crop of nauplii may have been impoverished by the removal of a great number of eggs.

Though the phytoplankton must also be affected by the losses, the total volume of the algae was very high in 1959. The reproduction rate of many algae is, however, very fast compared to the zooplankton and as I have already mentioned the primary production was very high compared to the production in 1955 when the standing crop was also impoverished by outflow losses. It may therefore be assumed that in 1959 the primary production and the reproduction rate of the species was high enough to replace the losses, while this was not the case in 1955.

The statement that the crustaceans may to some extent withstand the draw from a lake ought to be discussed in some respects. Supposing that there is a constant flow of water towards the outlet the animals do not show evasive responses until there is a certain current gradient. EINSELE (1960) reports that at a current velocity of 3 cm/sec the crustaceans can not withstand the current but are brought away in conformity with the dead particles of the water. Within the variations of the discharge in Ransaren a current velocity of 3 cm/sec may not appear until very near the outlet. At a current velocity below 3 cm/sec but higher than 1 cm/sec the crustaceans may swim actively against the current to avoid being swept away by the outflow. A concentration of animals is thus to be expected in the area of a lake where the current is rapid enough to be perceived by the animals, but slow enough to make it possible for them to evade the outflow. In Ransaren a current velocity of 1—3 cm/sec is reached in the region between the dam and station 1. Unfortunately no plankton profiles have been taken in this area of Ransaren. It is possible, however, that the abnormally high values of adult crustaceans at station 1 on July 20, 1959 was not only caused by the normal water movements of the lake, but also by a concentrating effect of the draw.

In 1960 the total volume of the zooplankton did not differ significantly from the values of 1959. There was, however, a marked change in the composition of the zooplankton. The rotifer population was so small that the

volume could not even be plotted on the diagram. The dominance of southerly winds during the whole summer implies that a surface transport of water in a northerly direction may to some extent have contributed to the decrease. However, as it is very likely that the effect of a high discharge during the growth period of one year may also influence the growth during a following year, the low values for particularly the epilimnic rotifers in 1960 may also be due to the draw in 1959.

I will summarize by saying that the regulation of Ransaren has caused a considerable increase in the number of organisms as well as of the total volume of the zooplankton. The increase is most probably due to two different factors, one being improved food conditions, the other a reduction of the losses due to an almost complete closing of the lake in the summers of full impoundment. The investigation has also shown that the variations of the zooplankton in Ransaren are to a considerable extent affected by the variations in the rate of discharge from the lake.

As I have already mentioned, the standing crop of zooplankton in Kultsjön remained practically unchanged through all the years of the investigation. The recorded changes are almost entirely within the limits of the natural variations. In 1954 and 1960 only three vertical series were taken, the results from these years are thus quite uncertain. In the series from July 22, 1960 the number of *Daphnia galeata* is remarkably high and so is consequently the total volume. Due to an accident the samples from 5 and 10 m were lost and an interpolation between the samples from 1 and 20 m is very hazardous. Though the possibility of a regulation effect must not be disregarded, the recorded high value of only one species at only one occasion may indicate that the value is not caused by the impoundment of the lake.

Conclusions

Because of the variations in the water supply one can not expect the upper limit of the regulation in Ransaren to be reached every year. It is therefore possible that the variations in the zooplankton will proceed for an indefinite number of years and that a new lasting balance in the productivity of the lake will never be reached. The present investigation covers only a small period of the development of the impounded lake and further changes may occur in the future.

The bottom fauna which makes up the principal food of the trout and the char is seriously affected by a regulation. Particularly the char may switch to a zooplankton diet thus compensating for the decrease of the bottom fauna (GRIMÅS, NILSSON, RUNNSTRÖM, op. cit.). In the present paper I have shown that a sudden draw during the growth period impoverishes the zooplankton. From the point of view of fishery management, I therefore find

it necessary to point out, that a high discharge during the growth season ought to be avoided. Maintenance works requiring a lowering of the water level may therefore advantageously be performed in late autumn.

Acknowledgement

First of all I would like to express my gratitude to my teacher in limnology, Professor WILHELM RODHE, who has been responsible for the performance of the whole investigation and who has given me much valuable advice in the treatment of the material. I will also express my thanks to the other members of the investigation, RUNE RAGNBERG, ARNOLD NAUWERCK, LARS KARLGREN and ÖSTEN LINDGREN for putting their material at my disposal; to Dr. BIRGER PEJLER for giving me advice concerning some rotifer problems; to my wife and other participators in the field work; and to Mrs. BIRGITTA SANDBERG for revisal of the manuscript.

Summary

The zooplankton of two lakes in Northern Sweden, Ransaren and Kultsjön, has been investigated. Beside the studies of general zooplankton problems special attention has been given to the regulation of Ransaren and the changes in the zooplankton that might be due to the disturbance of the water level. The zooplankton values from Kultsjön have mainly been used as a reference material in order to exclude, as far as possible, the changes that are due to the natural variation.

In all, 33 species have been observed, many of which are quite rare. The following species are dominating in the open water: *Cyclops scutifer*, *Diatomus laticeps*, and *D. graciloides* among the copepods; *Daphnia galeata* among the cladocerans and *Polyarthra vulgaris*, *Kellicottia longispina*, *Conochilus unicornis*, and *Keratella cochlearis* among the rotifers.

The investigation of the horizontal and vertical distribution of the species has shown that the water movements are of vital importance. A surface transport of water may produce zones of unequal productivity and concentrate the zooplankton in one end of the lake. The swinging of the thermocline in the case of internal seiches sometimes changes the vertical position of the species to such an extent that the migratory movements of the animals are overruled.

In the littoral zone zooplankton swarms have been observed which to some extent may have been caused by the regulation.

Due to the regulation of Ransaren the environmental conditions have become more favourable and in 1957 and particularly in 1958, when the im-

poundment almost reached the upper limit for the regulation, a marked increase of the number of individuals took place. This increase is not only caused by improved environmental conditions but can also be ascribed to reduced losses in the summers when the lake was almost completely closed.

The discharge from the lake seems to play a considerable rôle in regulating the abundance of the epilimnic species. Particularly during the growth season the draw off of water impoverishes the plankton which may also result in deteriorated food conditions for the fish.

In Kultsjön the standing crop of zooplankton has remained unchanged through all the years. Thus no effect of the regulation of the lake in the period 1958—1960 has been observed.

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Table appendix

In the following tables some quantitative values are presented. Due to the consideration of space only a few series can be given. As only a few quantitative values from winter, spring, and autumn have been dealt with in the text there is need for some further information about these seasons. As a great part of the paper deals with the conditions in the summer of 1958 the most important series from this summer are also given. Concerning other vertical series the reader is referred to chapter V where a great many data can be found.

Zooplankton Ransaren, station 1, 1957. Ind/5 l.

Date:	11/1					14/5					28/10					
	1	5	10	20	30	1	5	10	15	20	35	1	5	10	20	37
COPEPODA																
Nauplii Centropagidae	—	—	—	—	—	2	3	1	2	3	—	—	—	—	—	—
— Cyclopidae	9	50	108	25	50	50	20	28	26	—	—	75	59	52	68	31
Copepoditer Diaptomus	—	—	—	—	—	4	5	1	2	1	—	—	—	—	—	—
— Cyclops	1	3	7	1	5	16	5	4	2	5	2	4	5	4	9	5
Cyclops scutifer ♀	—	1	—	—	—	8	2	—	—	—	—	—	—	—	—	—
CLADOCERA																
Holopedium gibberum ♀	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Daphnia galeata juv.	—	—	—	—	—	2	1	—	—	—	—	—	1	—	1	—
— ♂	—	—	—	—	—	—	—	—	—	—	—	2	2	1	5	3
— ♀	—	—	—	—	—	—	—	—	—	—	—	2	1	1	—	—
Bosmina obtusirostris ♂	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	1
— ♀	—	1	2	—	—	—	—	—	—	—	—	—	—	—	—	1
Chydorus sp.	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
ROTATORIA																
Synchaeta pectinata	—	—	—	—	—	—	—	—	—	—	—	2	7	2	5	2
— truncata	—	—	—	—	—	—	1	1	—	1	3	14	9	15	1	1
Polyarthra vulgaris + dolichoptera	6	7	1	0	3	—	—	1	—	1	1	18	18	28	18	14
Keratella cochlearis	5	11	26	3	10	26	22	6	23	28	1	45	39	43	73	43
— hiemalis	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—
Kellicottia longispina	42	107	118	29	62	36	25	17	34	33	7	80	92	65	135	104
Asplanchna priodonta	11	4	2	—	6	—	4	—	2	2	—	82	96	72	39	68
Conochilus unicornis	1	4	—	2	—	—	2	2	—	—	—	26	21	4	13	1
Filinia terminalis	1	2	—	—	—	—	—	—	1	—	—	5	5	6	8	4
Collotheca mutabilis	—	—	—	—	—	—	—	—	—	—	—	1	—	—	2	—

Zooplankton Ransaren, station 1, 1958. Ind/5 l.

Date:	11/1						5/4						19/5					
	1	5	10	20	40	47.5	1	3	5	10	20	40	1	5	10	20	41	
COPEPODA																		
Nauplii Centropagidae	—	—	—	—	—	—	67	47	8	7	4	1	—	5	7	2	—	
— Cyclopidae	3	33	36	38	63	160	295	98	164	35	15	41	181	42	20	14	44	
Copepoditer Diaptomus	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3	1	—	
— Cyclops	2	7	13	6	1	5	194	9	8	4	3	3	40	41	6	—	2	
Cyclops scutifer ♂	—	—	—	—	—	—	3	—	—	—	—	—	—	2	—	—	—	
— ♀	—	—	—	—	—	—	—	—	—	—	—	—	1	13	1	—	—	
CLADOCERA																		
Daphnia galeata juv.	—	3	2	—	1	4	—	—	—	—	—	—	4	5	8	—	—	
— ♀	—	—	—	—	—	—	3	2	2	1	—	1	—	13	4	—	—	
ROTATORIA																		
Synchaeta truncata	1	1	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	
Polyarthra vulgaris+	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	1	—	
dolichoptera	5	11	7	1	2	1	—	—	—	—	—	—	—	—	—	—	—	
Keratella cochlearis	4	16	17	43	28	24	115	26	52	6	8	2	3	31	13	3	—	
Kellicottia longispina	11	55	42	32	8	12	324	35	13	7	—	—	6	22	5	1	—	
Asplanchna priodonta	47	26	43	7	2	1	—	—	—	—	—	—	1	—	—	—	—	
Conochilus unicornis	2	1	2	—	3	—	—	—	—	—	—	—	—	—	4	—	—	
Filinia terminalis	—	8	1	—	—	—	—	3	1	—	1	—	3	12	2	—	—	

Zooplankton Ransaren, station 1, 1958. Ind/5 l.

Date:	1/7					15/7					1/8				
	1	5	10	20	40	1	5	11	20	40	1	5	10	20	45
COPEPODA															
Nauplii Centropagidae	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
— Cyclopidae	1	3	5	—	—	26	19	30	29	5	58	85	53	112	64
Copepoditer Diaptomus	—	—	—	—	—	4	1	—	—	—	—	—	—	—	—
— Cyclops	—	7	1	1	—	5	35	83	19	11	10	10	10	9	18
Diaptomus laticeps ♂	—	—	—	—	—	—	2	—	—	—	1	1	3	8	1
— ♀	—	—	—	—	—	—	3	1	—	1	2	2	2	1	1
— ♀, with eggs	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Heterocope cop	—	—	—	—	—	6	3	1	—	—	—	—	—	—	1
Cyclops scutifer ♂	—	—	—	—	—	—	2	—	2	1	6	2	5	3	3
— ♀	—	—	—	—	—	—	2	1	1	—	—	—	—	2	1
— ♀, with eggs	—	—	—	—	—	5	4	6	—	—	—	—	1	—	3
CLADOCERA															
Holopedium gibberum juv.	2	1	—	—	—	1	3	5	—	—	—	—	—	—	—
— ♀	—	—	—	—	—	1	3	6	—	—	2	—	1	—	2
— ♀, with eggs	—	—	—	—	—	5	1	—	—	—	2	—	—	—	—
Daphnia galeata juv.	—	—	—	—	—	15	20	18	1	—	17	7	10	11	11
— ♀	—	—	—	—	—	—	6	4	1	—	7	5	11	5	8
— ♀	—	—	—	—	—	18	12	12	3	1	7	6	6	3	1
— ♀, with eggs	—	—	—	—	—	5	4	2	—	—	—	1	1	—	—
Bosmina obtusirostris juv.	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
— ♀	—	—	—	—	—	1	1	2	—	1	—	—	1	—	—
ROTATORIA															
Synchaeta pectinata	—	—	—	—	—	—	1	2	15	7	—	—	—	—	—
— truncata	1	3	—	—	—	—	—	—	—	—	—	3	—	3	—
Polyarthra vulgaris + dolichoptera	—	1	—	—	—	52	81	107	109	41	10	5	47	26	3
Keratella cochlearis	1	—	—	—	—	—	—	6	89	18	33	30	28	116	72
— hiemalis	—	—	—	—	—	—	—	—	1	1	—	—	—	2	—
Kellicottia longispina	1	2	1	—	—	71	125	161	79	21	18	33	41	30	22
Asplanchna priodonta	—	—	—	—	—	—	1	—	2	2	—	1	—	—	—
Conochilus unicornis	—	—	1	—	—	227	126	212	17	54	—	1	30	30	4
Filinia terminalis	—	3	—	—	—	—	—	—	16	8	2	4	4	20	4
Collotheca mutabilis	—	—	—	—	—	2	3	2	3	—	1	2	—	1	1
Rotatoria ssp.	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—

Zooplankton Ransaren, station 2, 1958. Ind/5 l.

Date:	1/7					17/7					31/7				
	1	5	10	20	40	1	5	10	20	40	1	5	10	20	45
COPEPODA															
Naupli Centropagidae	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
— Cyclopidae	38	11	9	1	—	14	13	15	11	10	4	65	35	20	62
Copepoditer Diaptomus	39	13	1	—	—	—	—	—	—	—	—	—	—	—	—
— Cyclops	30	117	20	6	1	8	16	10	25	23	1	41	74	55	19
Diaptomus laticeps ♂	—	—	—	—	—	—	1	—	—	1	1	2	1	—	1
— — ♀	13	—	—	—	—	1	1	—	2	—	3	1	—	—	—
— — ♀, with eggs	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Heterocope cop.	3	—	—	—	—	—	—	—	—	—	—	2	2	—	—
Cyclops scutifer ♂	7	12	—	—	—	—	2	—	1	1	—	10	8	12	1
— — ♀	6	6	1	—	—	—	—	—	—	—	—	6	8	7	—
— — ♀, with eggs	6	6	—	—	—	1	—	—	—	—	—	1	1	1	2
GLADOCERA															
Holopedium gibberum juv.	16	2	—	1	1	—	—	—	—	—	—	—	—	—	—
— — ♀	1	—	—	—	—	—	—	—	1	—	1	2	5	5	1
— — ♀, with eggs	—	—	—	—	—	—	—	—	—	—	—	—	3	5	1
Daphnia galeata juv.	35	14	—	—	2	6	5	4	4	8	—	34	23	28	14
— — ♀	—	—	—	—	—	3	1	—	5	2	1	2	2	1	3
— — ♀	16	7	—	—	—	1	3	4	4	1	1	28	21	21	6
— — ♀, with eggs	17	5	1	—	—	—	1	—	1	1	—	2	4	2	5
Bosmina obtusirostris ♀	4	3	—	—	—	1	2	1	2	1	—	3	2	—	—
— — ♀, with eggs	—	—	—	—	—	—	—	—	—	—	1	—	3	—	—
ROTATORIA															
Synchaeta pectinata	3	13	—	—	—	7	4	2	1	—	—	—	—	—	—
— truncata	—	3	—	—	—	3	3	3	2	3	—	—	—	2	2
Polyarthra vulgaris+															
dolichoptera	52	10	3	3	—	28	38	57	34	17	188	154	157	75	39
Keratella cochlearis	30	37	14	12	3	19	15	20	24	15	3	7	2	5	12
Kellicottia longispina	59	59	2	5	—	52	31	34	16	31	166	243	254	232	112
Asplanchna priodonta	1	—	—	—	—	—	1	—	2	1	—	—	—	—	—
Conochilus unicornis	15	16	3	16	—	4	9	32	20	13	359	208	91	134	12
Filinia terminalis	—	29	2	4	1	3	2	8	3	6	—	—	—	—	—
Collotheca mutabilis	2	2	1	—	—	2	—	2	3	1	1	2	1	—	—

Zooplankton Ransaren, station 2, 1958. Ind/5 l.

Date:	17/8					2/9				
	1	5	10	20	45	1	5	10	20	45
COPEPODA										
Nauplii Cyclopidae	—	3	476	135	6	25	107	295	322	12
Copepoditer Cyclops	4	11	—	5	20	2	1	10	7	11
Diaptomus laticeps ♂	—	—	—	1	—	1	1	—	—	—
— — ♀	—	—	—	1	—	—	—	1	—	—
— — ♀, with eggs	—	—	2	—	—	2	1	2	1	—
Hetercope saliens ♂	1	—	—	—	—	1	—	—	—	—
Cyclops scutifer ♂	5	25	7	—	1	8	3	7	—	—
— — ♀	3	41	2	3	—	8	1	2	—	2
— — ♀, with eggs	3	17	—	—	—	12	5	22	3	—
CLADOCERA										
Holopedium gibberum ♀	5	5	—	—	—	—	1	—	—	—
Daphnia galeata juv.	—	4	—	—	1	—	—	—	—	—
— — ♂	—	1	—	1	—	—	—	—	1	1
— — ♀	—	12	3	—	—	—	2	2	2	—
— — ♀, with eggs	—	4	1	—	—	—	2	2	1	—
Bosmina obtusirostris ♀	3	2	—	—	—	5	2	—	2	—
— — ♀, with eggs	2	—	—	—	—	4	—	—	—	—
ROTATORIA										
Synchaeta pectinata	—	—	3	—	—	—	—	—	—	—
— truncata	3	—	—	1	1	25	40	3	7	—
Polyarthra vulgaris + dolichoptera ..	32	6	9	4	7	294	224	25	15	8
Keratella cochlearis	3	5	185	54	4	19	34	105	129	7
Kellicottia longispina	106	129	71	95	8	637	405	98	26	19
Asplanchna priodonta	—	—	—	—	1	—	—	—	1	—
Conochilus unicornis	198	22	23	—	4	78	145	356	162	7
Filinia terminalis	—	—	3	13	4	—	—	16	14	9
Collotheca mutabilis	—	—	3	—	—	35	8	4	5	—
Rotatoria spp.	—	—	—	—	—	1	—	—	—	—

Zooplankton Kultsjön, station 1, 1957. Ind/5 l.

Date:	12/1					13/5					24/10				
	1	5	10	20	41	1	5	10	20	41	1	5	10	20	40
COPEPODA															
Nauplii Cyclopidae	—	2	5	77	13	40	53	26	16	35	17	20	19	18	19
Copepoditer Diaptomus	—	—	—	—	—	12	8	12	1	—	—	—	—	—	—
— Cyclops	1	—	1	1	2	5	1	—	—	—	2	2	2	1	—
Diaptomus graciloides ♂	—	—	—	1	1	—	3	—	—	—	—	1	—	—	—
— ♀	—	—	—	—	—	—	1	—	—	1	—	—	—	1	1
Cyclops scutifer ♂	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
— ♀	1	—	2	—	—	6	1	—	—	—	—	—	—	—	—
CLADOCERA															
Daphnia galeata juv.	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
— ♂	—	—	—	—	—	—	—	—	—	—	2	—	—	2	—
Bosmina obtusirostris ♂	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
— ♀	—	—	—	—	—	1	—	1	—	—	2	—	—	—	—
ROTATORIA															
Synchaeta truncata	—	—	—	—	—	—	—	—	—	—	—	1	—	3	1
Polyarthra vulgaris+dolichoptera ..	1	6	1	—	6	1	1	—	—	—	3	—	—	1	2
Keratella cochlearis	7	26	3	—	9	—	8	—	—	—	10	9	3	9	5
— hiemalis	—	3	1	1	2	—	1	—	—	—	—	—	—	—	—
Kellicottia longispina	16	29	31	3	7	3	10	8	—	—	11	22	3	20	4
Conochilus unicornis	—	—	—	—	—	—	—	—	—	—	4	2	—	—	1
Filinia terminalis	—	—	1	—	—	—	—	—	—	—	1	6	—	1	1

Zooplankton Kultsjön, station 1, 1958. Ind/5 l.

Date:	8/4					20/5					19/6					
	1	3	5	10	20	40	1	5	10	20	41	1	5	10	20	45
COPEPODA																
Nauplii Centropagidae	9	8	8	4	1	—	—	10	14	1	—	2	13	4	12	5
— Cyclopidae	1	—	2	8	36	31	3	6	12	11	25	5	30	19	23	25
Copepoditer Diaptomus	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—
— Cyclops	13	5	—	1	—	—	1	1	—	—	—	5	1	—	1	1
Diaptomus graciloides ♂	—	—	—	—	—	—	—	1	—	—	—	1	1	1	2	—
— ♀	2	2	2	—	—	—	—	—	—	—	—	—	1	1	2	—
— ♀, with eggs	—	—	1	1	—	—	—	—	—	—	—	—	1	—	—	1
Cyclops scutifer ♂	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
— ♀	2	1	—	—	—	—	—	1	—	—	—	1	—	—	—	—
CLADOCERA																
Daphnia galeata juv.	—	—	—	—	—	—	—	1	1	—	1	—	—	—	—	—
— ♀	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—
Bosmina obtusirostris ♀	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	—
ROTATORIA																
Synchaeta truncata	—	—	1	—	—	—	—	1	—	—	—	—	1	1	—	—
Polyarthra vulgaris+dolichoptera ..	8	3	1	—	1	—	—	1	—	—	—	—	—	1	—	—
Keratella cochlearis	13	13	5	1	—	—	3	12	—	—	—	1	6	3	3	5
— hiemalis	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Kellicottia longispina	85	27	16	3	1	1	21	16	9	2	—	2	5	5	6	1
Conochilus unicornis	—	2	—	1	3	—	1	—	—	—	—	1	—	3	—	—
Filinia terminalis	6	—	—	—	—	—	2	—	—	—	—	—	—	1	1	—

Zooplankton Kultsjön, station 1, 1958. Ind/5 l.

Date:	2/7					16/7					30/7				
	1	5	10	20	41	1	5	10	20	40	93 ¹⁾	1	5	10	40
COPEPODA															
Nauplii Centropagidae	8	21	69	2	—	16	9	16	16	15	—	4	3	1	2
— Cyclopidae	3	1	11	2	1	11	5	8	4	5	—	9	10	13	13
Copepoditer Diaptomus	1	1	1	—	—	11	10	8	19	8	2	21	14	8	19
— Heterocope	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
— Cyclops	—	12	47	5	2	14	5	8	10	6	1	5	6	10	—
Diaptomus graciloides ♂	11	5	—	—	—	—	—	1	—	—	—	—	—	—	—
— — ♀	2	—	—	—	—	1	1	—	—	—	—	—	—	—	—
— — ♀, with eggs	3	3	—	—	—	—	—	—	—	—	—	—	—	—	—
Cyclops scutifer ♂	—	1	—	—	—	1	—	1	1	—	—	2	1	—	—
— — ♀	2	—	—	—	—	—	—	—	—	—	—	1	1	—	1
— — ♀, with eggs	—	—	—	—	—	1	1	—	1	—	—	—	1	—	—
CLADOCERA															
Holopedium gibberum juv.	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—
— — ♀	—	—	—	—	—	2	2	1	3	—	—	—	—	—	—
— — ♀, with eggs	—	—	—	—	—	1	—	—	—	—	—	—	1	—	—
Daphnia galeata juv.	—	—	—	2	—	5	1	2	3	1	—	—	—	—	1
— — ♀	—	—	—	—	—	6	—	1	—	—	—	—	—	1	1
Bosmina obtusirostris ♀	3	1	—	—	—	2	5	3	6	—	—	1	—	2	1
— — ♀, with eggs	—	1	—	—	—	—	1	—	1	—	—	—	1	—	—
ROTATORIA															
Synchaeta pectinata	—	—	—	—	—	5	6	5	5	6	2	—	—	—	—
— truncata	2	5	1	—	—	—	—	—	—	—	—	1	1	2	2
Polyarthra vulgaris + dolichoptera	2	6	—	—	—	10	5	8	2	4	—	7	11	9	9
Keratella cochlearis	3	10	—	—	—	12	16	9	12	11	2	17	19	20	10
Argonotholca foliacea	—	—	—	—	—	—	—	—	—	1	—	1	—	—	—
Kellicottia longispina	3	15	10	1	5	27	31	27	37	27	1	18	23	20	25
Asplanchna priodonta	—	1	—	—	—	3	3	7	1	2	—	1	3	—	2
Ploesoma hudsoni	—	—	—	—	—	1	—	1	—	1	—	—	2	—	3
Conochilus unicornis	7	3	1	—	1	36	42	57	1	7	23	—	—	—	—
Filinia terminalis	1	4	2	1	2	—	—	1	1	2	—	—	1	—	—
Collotheca mutabilis	—	—	—	—	—	3	—	—	—	—	1	—	—	—	—

¹ This sample is taken in the deepest part of the western basin of Kultsjön.

Zooplankton Kultsjön, station 1, 1958. Ind/5 l.

Date:	16/8					29/8					8/11				
	1	5	10	20	40	1	5	10	20	40	1	5	10	20	40
COPEPODA															
Nauplii Centropagidae	5	6	—	—	—	3	2	—	—	—	1	—	—	—	—
— Cyclopidae	3	11	15	14	8	11	8	6	12	8	16	24	23	39	29
Copepoditer Diaptomus	8	180	5	—	—	11	15	7	12	—	—	—	—	—	—
— Hetercope	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—
— Cyclops	1	4	2	26	14	1	—	2	24	15	7	6	10	12	9
Diaptomus graciloides ♂	2	2	2	—	—	—	1	—	—	—	—	2	—	—	—
— ♀	—	—	—	—	—	6	1	7	—	1	1	3	1	2	1
— ♀, with eggs	—	2	1	—	—	—	—	—	—	—	—	—	—	—	—
Cyclops scutifer ♂	1	1	—	—	—	3	2	3	—	1	—	—	—	—	—
— ♀	1	2	—	—	—	1	1	1	—	—	—	—	—	—	—
— ♀, with eggs	—	2	—	—	—	—	1	1	—	—	—	—	—	—	—
CLADOCERA															
Holopedium gibberum ♀	2	4	—	—	—	—	1	1	2	—	—	—	—	—	—
— ♀, with eggs	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Daphnia galeata juv.	3	2	3	1	—	—	—	—	1	—	—	—	—	—	—
— ♂	4	1	1	—	—	1	3	4	1	—	—	—	—	—	—
— ♀	1	5	—	—	—	—	8	2	3	4	—	—	—	—	—
— ♀, with eggs	2	—	1	—	—	1	1	—	—	—	—	—	—	—	—
Bosmina obtusirostris juv.	—	—	—	—	—	—	—	—	2	3	—	—	—	—	—
— ♀	13	4	3	3	5	3	—	3	4	—	—	—	—	—	—
— ♀, with eggs	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
ROTATORIA															
Synchaeta pectinata	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
— truncata	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—
Polyarthra vulgaris + dolichoptera	2	16	11	1	—	36	39	12	1	24	3	10	5	18	11
Keratella cochlearis	2	9	35	12	5	16	8	7	10	12	3	10	6	6	7
— hiemalis	—	—	—	—	—	—	—	—	—	—	—	—	1	2	1
Kellicottia longispina	13	45	54	14	2	103	79	17	40	45	4	12	13	8	9
Asplanchna priodonta	—	2	1	4	—	—	1	—	—	1	—	—	—	—	—
Conochilus unicornis	—	26	1	—	—	65	142	32	40	144	1	1	—	6	—
Filinia terminalis	—	—	—	2	—	—	—	—	—	—	—	—	1	3	—
Collotheca mutabilis	1	—	—	1	—	2	1	1	—	1	—	—	—	—	—

Zooplankton Kultsjön, station 2, 1958. Ind/5 l.

Date:	28/6					29/7					27/8			
	1	5	10	20	40	1	5	10	20	40	1	10	20	40
COPEPODA														
Nauplii Centropagidae	—	8	5	11	9	10	5	—	—	—	2	—	—	—
— Cyclopidae	—	3	4	5	5	7	3	9	4	—	18	5	43	13
Copepoditer Diaptomus	1	—	1	—	—	24	10	2	19	3	7	12	3	1
— Heterocope	—	—	—	—	—	—	—	—	—	—	2	1	1	—
— Cyclops	8	37	8	7	1	13	17	17	15	18	1	7	4	2
Diaptomus graciloides ♀	2	—	—	—	—	2	1	1	2	1	2	3	—	—
— ♀, with eggs	1	—	—	—	—	—	—	—	—	—	—	—	—	—
— laticeps ♀	—	—	—	—	—	—	—	—	—	—	—	—	1	—
— ♀, with eggs	—	—	—	—	—	—	—	—	1	—	—	—	—	—
Cyclops scutifer ♂	—	1	—	—	—	—	1	—	1	1	1	8	—	—
— ♀	3	1	—	—	—	1	2	—	—	2	—	3	3	1
— ♀, with eggs	—	—	—	—	—	—	—	—	—	—	—	5	—	—
CLADOCERA														
Holopedium gibberum ♀	—	—	—	—	—	1	—	—	1	—	—	1	—	—
— ♀, with eggs	—	—	—	—	—	—	—	—	—	—	—	1	—	—
Daphnia galeata juv.	—	1	—	—	—	4	2	—	2	—	—	1	1	—
— ♀	2	—	—	—	—	4	1	—	—	—	—	2	1	—
Bosmina obtusirostros ♀	2	—	—	—	—	1	2	—	2	—	5	3	6	3
ROTATORIA														
Synchaeta truncata	—	—	2	1	—	2	1	3	—	6	—	—	1	—
Polyarthra vulgaris + dolichoptera	—	—	—	—	—	27	14	5	36	1	5	12	1	—
Keratella cochlearis	1	5	4	2	—	9	12	23	19	19	4	2	31	12
Kellicottia longispina	7	7	3	4	—	28	50	16	35	5	99	102	36	17
Asplanchna priodonta	—	—	—	1	—	1	—	2	—	—	—	—	—	1
Ploesoma hudsoni	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Conochilus unicornis	1	—	—	—	—	67	57	1	—	1	—	—	—	—
Filinia terminalis	1	—	—	—	—	1	—	—	—	—	—	—	2	—
Collotheca mutabilis	—	—	—	—	—	—	1	—	1	—	1	—	—	—

On the dimorphism in *Cyclops scutifer* (SARS) and the cyclomorphosis in *Daphnia galeata* (SARS)

By JAN AXELSON

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In my studies of the zooplankton in the lakes Ransaren and Kultsjön in northern Sweden (AXELSON, 1961) I have come into contact with some special problems concerning the biology of the copepod *Cyclops scutifer* and the cladoceran *Daphnia galeata*. The material is obtained from quantitative and qualitative samples that were taken in the summer of 1957 and 1958. The present paper is only a minor part of the zooplankton investigation that was carried out in the two lakes in the years 1954—1960. The reader is therefore referred to the above mentioned paper in order to obtain a description of the lakes as well as further information about the zooplankton.

Cyclops scutifer (SARS)

This species is very widely distributed in Scandinavia. In many lakes of northern Sweden it is the only representative of the genus, so in Ransaren and Kultsjön. In some stage of development it can be found throughout the year.

In fig. 1 the curves for the standing crop of nauplii, copepodites and adults in the summer of 1958 in Ransaren have been drawn. The values refer to the total amount of individuals from the surface to the bottom of the lake under a surface area of 1 dm² at two different stations in the opposite ends of the lake.¹ When also studying the series that were taken in January, April, May and November the same year, it was clear that though more than one generation occurred in the lake, it was not a question of a simple succession. In order to follow the variations more closely, about 500 copepodites and 100 adults were therefore examined morphologically and measured. The measurements are made from preserved animals and make up the length from the top of the head to the end of the furca. No notice has been taken of the length of the furcal spines.

From the results of the measurements the following can be concluded. There seem to be two different fractions in Ransaren which differ from each other by their different size and annual cycle. The morphological features of the two types are exactly the same with the exception of the size. A dualism in

¹ The depth at the two stations varies around 40 m, and when constructing the diagrams this value has always been used.

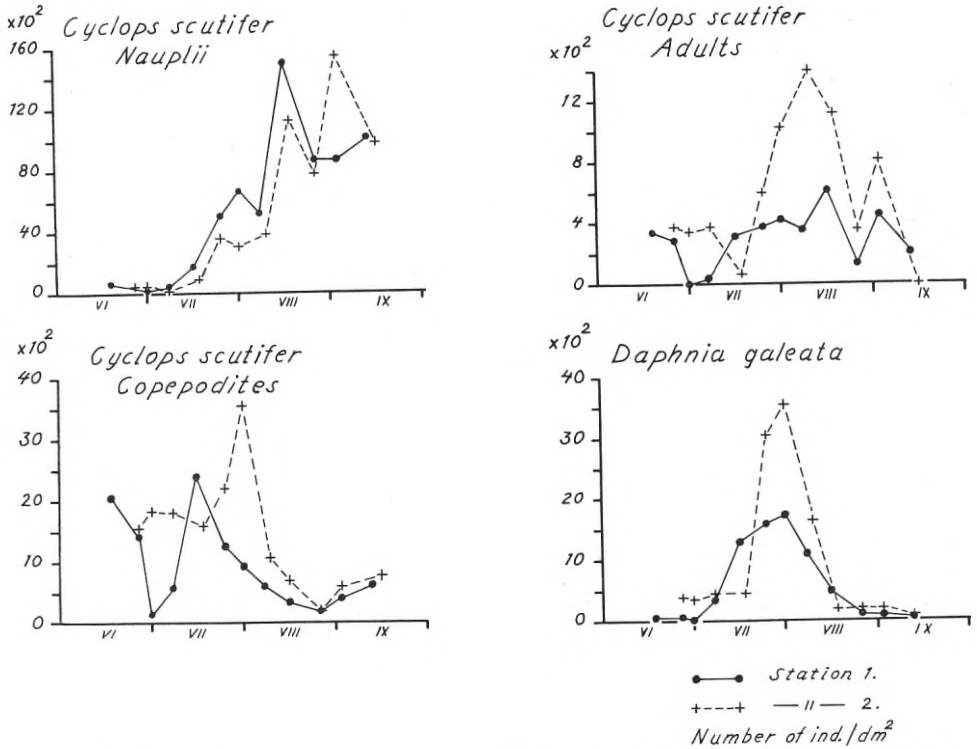


Fig. 1. The development of *Cyclops scutifer* and *Daphnia galeata* in Ransaren in 1958.

Cyclops scutifer has earlier been described from northern Sweden by LINDSTRÖM, who discusses it thoroughly in his papers from 1952 and 1958. The two types will be called fraction A and B which is in agreement with the terminology of LINDSTRÖM.

I will begin with a description of fraction A, which is most thoroughly studied. The results of the measurements of this fraction are presented in fig. 2.

From this diagram one easily notices that the copepodites are grouped around 4 different means, about 0.46, 0.59, 0.71 and 0.85 mm. Nauplii with a length of 0.4 mm have been observed which is the same value that has been found for the smallest copepodites. The value of 0.46 mm can thus be considered to be the mean length for the first copepodite stage. The other means represent stage II—IV, while stage V is completely undistinguishable. Thus there seems to be no difference in body length between the fifth stage and the adults. This is in agreement with the description of *Cyclops strenuus* made by RAVERA (1953). The two species are, as a matter of fact, very similar to each other. Further it can be concluded that stage V is smaller in the males than in the females. In the other four stages, however, there seems to exist no

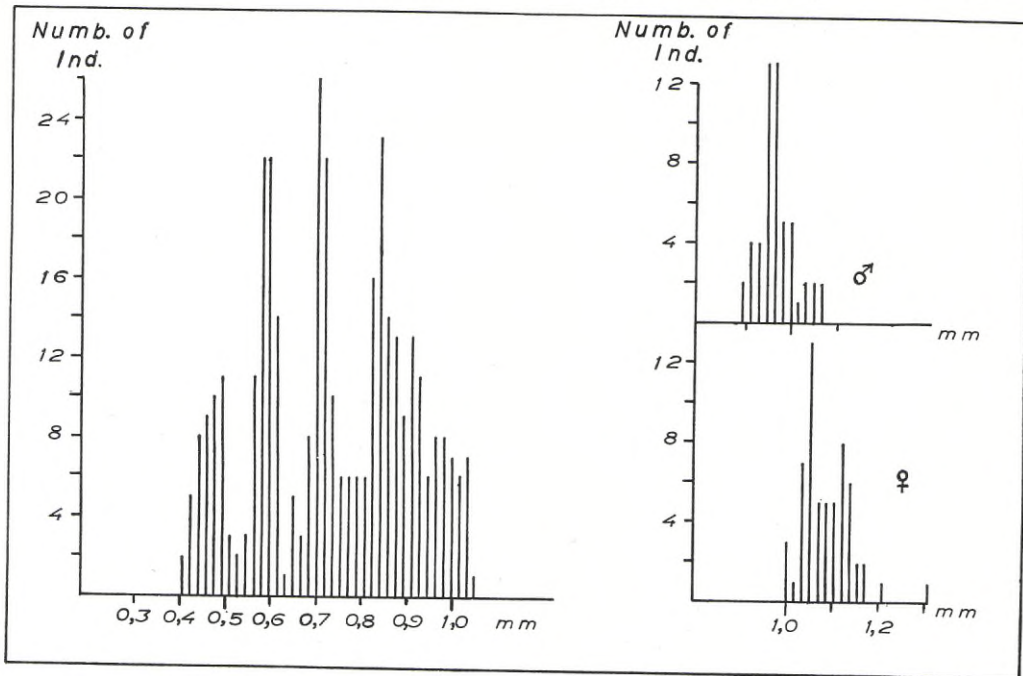


Fig. 2. Body length of copepodites (left) and adults (right) of *Cyclops scutifer* (fraction A) in Ransaren.

difference in length between males and females. This is confirmed by the countings, which show that the males and the females are of equal number, and the highest values in fig. 2 (left) must be considered to be made up of both sexes.

Although the number of adults which have been measured is indeed quite inconsiderable, it is interesting to find that they are of a very moderate size. Only two specimens among the females exceeded 1.2 mm, a value which by many authors is considered to be the lower limit for the sex (c.f. RYLOV 1935). The mean value is as low as about 1.1 mm. A striking fact is also the smallness of the males, the majority being less than 1.0 mm.

The annual cycle of fraction A will be the following. The adults have their maximum appearance in the later part of August, giving rise to a nauplii population, the development of which seems to be delayed during the winter due to the low water temperature (c.f. LINDSTRÖM 1958). The nauplii develop into copepodites at the time of the breaking up of the ice and pass the copepodite stages during July and the first part of August, and the cycle is finished with a new generation of adults. The duration of the ice-cover in spring probably affects the development of the nauplii into copepodites by a direct or indirect effect of the spring turn-over.

The other *scutifer* type in Ransaren, fraction B, does not show such a

regularity as fraction A. Adult females carrying eggs begin to appear in June and still in August a few can be found together with adults of fraction A. Their nauplii start their development in the later part of July and in the samples from September and October—November young copepodites are found. In the January samples only old copepodites seem to represent the type, which is also the case in April and May. I therefore conclude that fraction B passes the winter in a resting stage of old copepodites. Deviations from this principal course is not uncommon. Some of the copepodites, for example, may develop into adults already in late winter and the largest of the measured specimens are found in April with a length of 1.6—1.7 mm. With the exception of the annual cycle the most striking difference between this type and fraction A is their size. The males vary between 1.12—1.26 mm and the corresponding figures among the females are 1.26—1.68 mm, the majority being more than 1.3 mm. Only a few measurements have been made of the copepodites because of the insufficient number of samples taken in winter. The resting copepodites seem to vary around 0.96—1.25 mm, the values, however, being very uncertain. Just as uncertain is the possibility that both the fourth and the fifth copepodite stage serve as resting stages during the winter.

Although laboratory experiments are entirely lacking and the winter samples are very scarce, the dualism described above might be considered as proved. Thus if future investigation of *Cyclops scutifer* will further confirm this kind of dualism, I find it interesting that the same species in the same lake appears in two distinct types which are morphologically alike but differ from each other in their size and annual cycle. This phenomenon raises many questions, which can only be answered by laboratory experiments. I will therefore draw no further conclusions on the basis of the present material. Suffice it to say that there are no morphological indices that the two types represent different species.

The results presented above are in good agreement with the observations of LINDSTRÖM (cited above). The only deviation from his results is concerned with the origin of fraction A. LINDSTRÖM says that this fraction originates from a spring pulse of nauplii and young copepodites but makes a reservation as to the origin of the nauplii. However, it is my opinion that in Ransaren the nauplii originate from the egg-carrying females in August the preceding year, the nauplii thus functioning as a resting stage. The winter samples are indeed very few, but in all of them the nauplii are very rich in number and as there seem to exist no adults during the midwinter, these nauplii most probably originate from the above mentioned adults.

The *Cyclops scutifer* population in Kultsjön has also been studied. A number of specimen have been examined morphologically and measured in respect to their body length. Practically all individuals, which have been found from June to September correspond closely to fraction A in Ransaren.

The pronounced division into two distinct fractions, which has been described above from Ransaren, is not clearly distinguishable in Kultsjön. This, however, does not mean that fraction B does not occur in Kultsjön. The presence of old copepodites in the January samples as well as in the samples from May and the beginning of June indicates a divergence from the simple seasonal course of fraction A. However, Kultsjön has not been investigated to the same extent as Ransaren, and I therefore leave the question open as to whether or not a dualism in *Cyclops scutifer* is existant in Kultsjön.

Daphnia galeata (SARS)

Two *Daphnia* species have been found in Ransaren. They belong both to the *longispina* group as is easily seen by the post-abdominal characters and the presence of an ocellus. By using trinomials and sometimes even quadrinomials the *longispina* group is split up into a number of subspecies and varieties, which causes a very confusing taxonomy and it is still common to find different names of what is definitely the same species. Though it is beside the point to deal closely with the taxonomy of the genus *Daphnia* in this paper, I find it necessary in a few words to explain my own position to the question of the names of the most common species.

BROOKS (1957) has given an extraordinarily good description and taxonomic study of the North American *Daphnia* in which he, in every species save one, avoids the use of trinomials or more. Unfortunately his classification can not be used to a full extent in Europe, but it is my opinion that there is a great need for a similar treatment of the European species.

The most common species in Ransaren follows the ordinary course of cyclomorphosis with round-headed individuals in winter and those with pointed helmets in summer. This species is very often given the name *D. longispina* ssp. *hyalina* and sometimes a quadrinomial var. *galeata* is added to the name. *D. longispina* ssp. *hyalina* is not a good name as it includes both helmeted forms and those which are always round-headed. In order to be exact a fourth name is always necessary e.g. *galeata*. The head species of the *longispina* group *D. longispina* s.str. (O. F. MÜLLER) and *D. hyalina* s.str. (LEYDIG) are well defined species and according to SCOURFIELD and HARDING (1958) the form in Ransaren might be called *D. hyalina* var. *galeata* because of the close relationship to *hyalina* s.str. Yet, if the variety *galeata* is so distinctly separated from the head species *hyalina* s.str. that it always demands a third name, I can not see why it is necessary to use a trinomial instead of the simple name *D. galeata* (SARS).

EKMAN (1904), later cited by RYLOV (1935), describes a course in *D. longispina* ssp. *hyalina* or in this paper *D. galeata* meaning a development from the round-headed *microcephala* and *obtusifrons* types in winter and in spring to

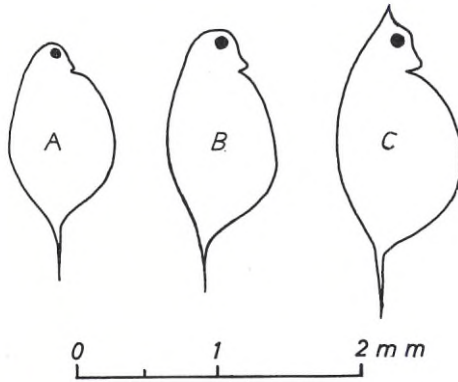


Fig. 3. *Daphnia galeata* in Ransaren.

A.=s.f. *microcephala*

B.=s.f. *obtusifrons*

C.=s.f. *galeata*

the *galeata* type in summer. The same variations have been found in Ransaren and Kultsjön but instead of using the term "variety" for the different types, I will in this paper use the term "seasonal forms" (abbreviated s.f.). I do so because the term variety, as a rule, is used to characterize morphological deviations from the species in a strict sense, that is to say in most cases to describe the morphological features of a *Daphnia* population, which is never identical with the head-species, and not to describe seasonal variations within the head species.

The description below is based on the material from Ransaren. As *Daphnia galeata* in Kultsjön does not differ from *D. galeata* in Ransaren the results may be considered to be valid also for Kultsjön.

A diagram of the quantitative variations in the summer of 1958 is presented in fig. 1. Only a small number of individuals is found in the beginning of the ice-free season. The population density gradually increases during July and the maximum is usually reached in the beginning of August. The number of individuals then rapidly declines but a few specimens are still found in the autumn.

A closer study of the annual cycle gives the following result. The resting eggs are hatched in late winter. The adults of this origin are quite small and belong to s.f. *microcephala* or *obtusifrons* (fig. 3).

Until the end of June and the beginning of July the population is entirely made up of these two seasonal forms. If there is more than one generation of the round-headed forms, I do not know. The subitan-eggs of these females are hatched after the break-up of the ice and give rise to a population of offspring with pointed helmets belonging to s.f. *galeata*. The general course is now that the juveniles grow up to males or to sexual females. The males often occur as early as in the middle of July. The subitan-eggs of the *microcephala* and *obtusifrons* females are, however, not hatched at the same time after the break-up of the ice, which means that there is no simple succession implying that the population during a fixed period is composed of juveniles in the same

stage of development. There is instead an overlapping in the appearance of the different stages. In most of the summer samples both adults and juveniles of different sizes can thus be found. Ephippial females producing resting-eggs occur as early as in the beginning of August but are still found in late autumn.

Deviations from this course are very common. The number of parthenogenetic generations as well as the appearance of males and sexual females are almost entirely depending on the weather conditions of the summer in question, and every response to changes in the water temperature must be regarded as normal. A warm summer for instance might increase the number of asexual generations. A study of the *Daphnia galeata* population in Ransaren in 1958 provides a very good example of this (fig. 4).

- June 18: Parthenogenetic females (s.f. microcephala)
 July 1: Parthenogenetic females (s.f. microcephala and obtusifrons).
 Young stages of s.f. galeata.
 July 7: Adult stages of all three seasonal forms. Juveniles of different
 stages (galeata). First appearance of males.
 July 15: Adult females (s.f. obtusifrons and galeata). Juveniles of
 different stages. Males.
 July 24: All stages of s.f. galeata. Males.
 August 1: The same including ephippial females.
 August 7: The same.
 August 15: The juveniles a little older. Males and ephippial females.
 August 25: Adult ephippial and parthenogenetic females. Almost adult
 females. Males.
 September 2: The same.
 September 12: Adult parthenogenetic females.
 November 6: Juveniles, parthenogenetic and ephippial females.

The observations mentioned above need to be explained in some respect. As a rule parthenogenetic females are not to be found as late as in the beginning of November. I can not explain this otherwise than that the unusual warming of the water during August and the short period of hot weather in September favoured a development of new asexual generations.

Daphnia galeata shows a marked cyclomorphosis in Ransaren and Kultsjön. In order to study this phenomenon more closely, a number of individuals have been measured. Before dealing with these results I will begin a short review of the literature of the cyclomorphosis in the genus *Daphnia*.

The pioneer in this field was WESENBERG-LUND, who in the beginning of the 20th century presented his "flotation—viscosity" theory in which he tried to explain the seasonal variation in *Daphnia* on the basis of the dependence of the viscosity on the water temperature. He meant that the round-headed cold-water form must be succeeded in summer by a form with larger

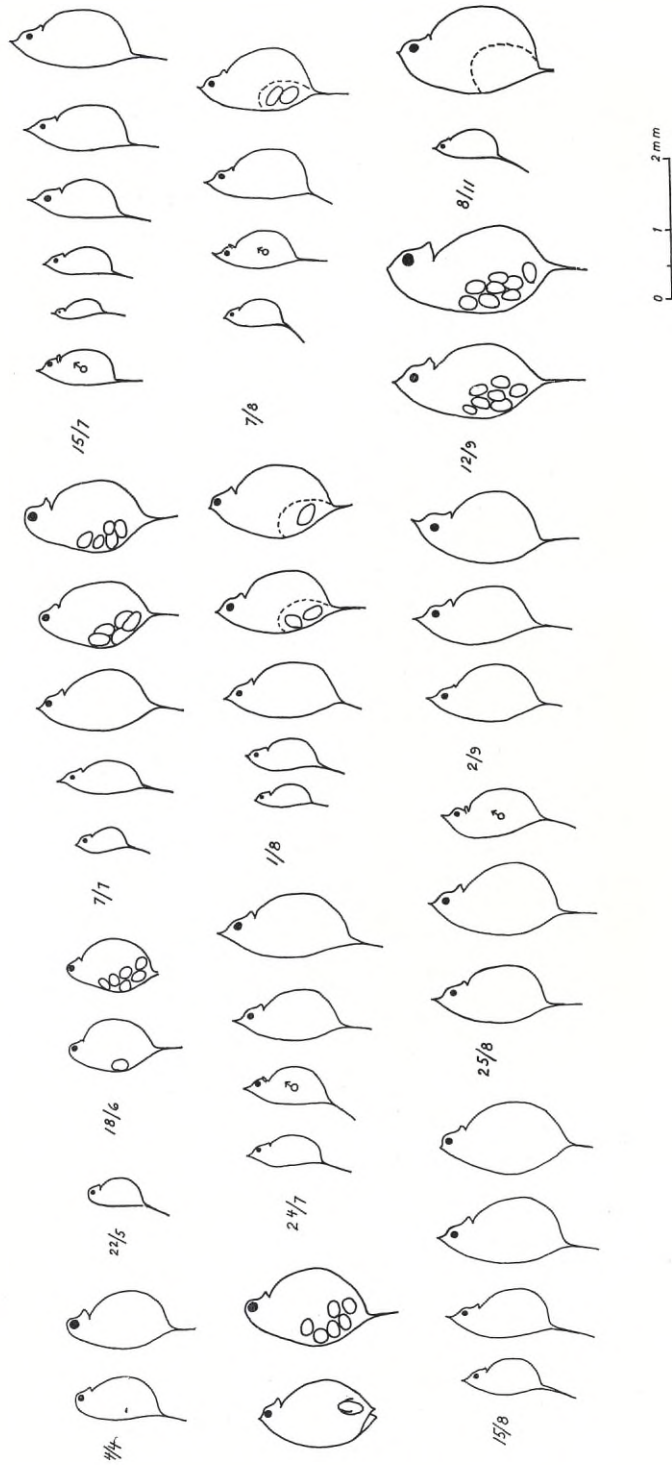


Fig. 4. Seasonal forms of *Daphnia galeata* in Ransaren.

projection area in order to avoid sinking in the less viscous water of higher temperature.

WOLTERECK suggested that the increasing parts of the body and the head served as stabilizers in order to keep the animals in the limited food layers of the summer water. He considered also the supply of food as well as the generation number to be the most important factors in bringing about a seasonal variation. His assumption that the first generation hatched from the resting-eggs must always be round-headed and that the helmet gradually grows with every new generation, has been refuted by BERG (1936) in laboratory experiments.

Practically all other investigations of the cyclomorphosis speak in favour of the temperature as the main factor in bringing about the seasonal variation in the morphology of the species, though not in accordance with WESENBERG-LUND. WAGLER (1936) presents a "vitality" theory which implies that there is an optimal state in the water to which the animals respond with maximum growth. This optimal state is supposed to depend mainly on the temperature. Any deviation above and below this optimum results in a decreasing growth.

The importance of the temperature is confirmed by OSTWALD (1904), COKER and ADDLESTONE (1938), and BROOKS (1946), though their results in the main do not correspond with those of WAGLER. The discovery that the temperature exerts its influence mainly during the embryonal period, was the most important result of their experiments.

BROOKS (1947) has also found a connection between the turbulence of the water and the development of a helmet. He has shown by laboratory experiments that *Daphnia* in an aquarium with agitated water developed almost the same type of helmets as they did in the lake, while the animals in unagitated water did not. A simultaneous control of the environmental conditions indicated a direct effect of the agitated water.

It must be considered a fact that the cyclomorphosis in the *Cladocera* must serve a special purpose. What this purpose might be or what brings about the seasonal variation is, however, not settled. Many are the explanations of this problem but this can be said: there seems to be a co-operation between several factors, two of which are the temperature and the turbulence of the water.

A study of the hitherto existing literature indicates that both round-headed and helmeted parthenogenetic females can give rise to different types of neonatae, which on their part develop into round-headed or helmeted adults. Even though the statement of WOLTERECK, that the ex-ephippial female must always be round-headed, now must be considered as incorrect, there seems to be a difference between the ex-ephippial neonatae and those originating from the subitan-eggs. The former are practically always round-headed and even the neonatae that were born in the laboratory experiment

by BERG (cited above) at such a high temperature as 22°C did not become helmeted until in the second and subsequent instars.

In Ransaren all the ex-ephippial stages are round-headed. The ephippia are always hatched when there is still an ice-cover on the lake and there seems to be a connection between the duration of the ice-cover and the development of helmeted neonatae.

In 1958 the first helmeted neonatae appeared in the later part of June at a temperature between 4 and 6°C and at such a low temperature cyclomorphosis is normally not considered to take place. So is also the case in November that year, when at a temperature of 5.4° small helmeted juveniles were found. It thus seems possible that the temperature only plays an inconsiderable rôle in bringing about helmet formation in *Daphnia* in Ransaren. There must be other active factors and the turbulence theory of BROOKS seems in this case to be very applicable. In the cold water of early summer and late autumn the lake is in a high degree of circulation and, as to water movements, the environmental conditions for the animals are the same as in the epilimnic water of the summer-stratified lake. If the turbulence thus would induce the formation of helmets it is to be expected that the helmets of the neonatae would be of the same size throughout the ice-free season, while the animals born in the relatively warm summer water would have bigger helmets if the temperature was the most important factor. In order to study the variations in helmets in the different generations of *D. galeata*, a number of animals have been examined microscopically and measured in respect to the length of the head and the carapace. The results are presented in fig. 5.

In this figure the values for head and carapace length (HL, CL) are plotted on a linear grid, where a double scale has been chosen for the y-axis. In so doing the diagram is much more easy to handle and though the difference in the slope of the lines will thus be accentuated, nothing is concluded that can not be made when using the same scale for both the axes.

The generic equation for a straight line is $y=kx+b$, where k is the slope of the line. When dealing with relative growth in *Daphnia*, $k < 1$ means that the head is growing more slowly than the carapace, $k=1$ that the growth is isometric and $k > 1$ that the head is growing faster than the carapace. In Ransaren k is always less than 1 being 0.58 for line A, 0.24 for line B, and 0.33 for line C.

The round-headed specimens of late winter—early summer, which are represented by the C-line consist entirely of adult females of *s.f. microcephala* and *obtusifrons*. The growth in the juvenile stages of these forms has not been calculated because of the lack of samples at the time of their appearance. Thus nothing more will be said than that the two round-headed forms differ from the helmeted *s.f. galeata* in the relative size of the head, the mean quotient $\frac{HL}{CL}$ being $\frac{0.29}{1.23}$ mm compared to $\frac{0.48}{1.27}$ mm in the adult and preadult stages of *s.f. galeata*.

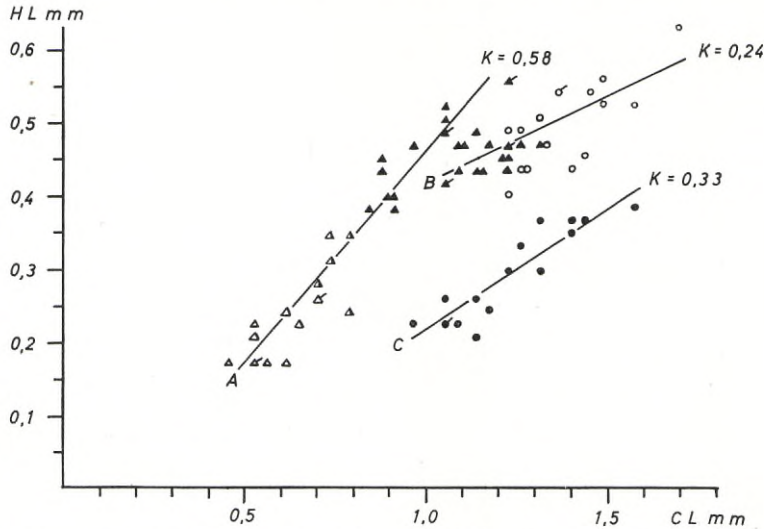


Fig. 5. Correlation between head length (HL) and carapace length (CL) in *D. galeata* in Ransaren.

- \triangle = small juveniles
 \blacktriangle = medium juveniles
 \blacktriangle = big juveniles
 \circ = adult females with spike heads
 \bullet = " " " round "
 $\triangle \blacktriangle \circ \bullet$ = more than one specimen

The measured animals are taken from samples from the whole ice-free season and it is interesting to find that the different generations did not differ from each other in respect to the relative head length, but individuals from quite different temperature environments could be plotted along the same line. Thus no marked difference could be found between the relative growth of the juveniles from July—August and from November. Yet there is a small decrease in the size of the helmets of the adult females in late autumn but this might depend more on a general deterioration in the environmental conditions than on a direct effect of any single factor.

Returning to the diagram we notice that the growth in the young stages follows a straight line with a k-value of 0.58. When reaching the pre-adult and the adult stages the relative growth is changed and now follows a new line, the k-value of which is 0.24. Because no exact point can be fixed for the shifting from line A to line B, it will be rather subjective to which line the values in the shift interval should belong. Yet there is no doubt that the relative growth is changed when the animal reaches the old stages and that this change is rather abrupt, the carapace length being about 1.05 mm.

A study of *Daphnia galeata* s.f. *galeata* in respect to water temperature has indicated that the relative growth of helmets in the neonatae and the sub-

Table 1. Water temperature in Ransaren 1958 at station 1.

	18.6	1.7	17.7	24.7	31.7	15.8	29.8	12.9
Surface	3.5	5.5	9.00	7.7	7.4	9.5	8.7	11.1
5 m	3.5	4.2	8.9	7.6	7.4	9.3	8.3	11.0
10 m	3.5	4.0	8.5	7.5	7.3	8.6	8.2	11.0
20 m	3.5	3.9	8.3	7.3	7.2	8.1	8.1	10.4
40 m	3.5	3.8	5.9	6.8	7.0	7.2	7.9	8.4

sequent instars do not vary with the temperature, but seems to be very constant throughout the ice-free season. In the adults a small decrease in the relative size of the points of the helmets appears in early autumn but neither in this case the changes can be correlated with the temperature conditions. The temperature values for September are higher than the corresponding figures for July (tab. 1).

To the table above one ought to add that there are great variations between different parts of the lake due to transport of water. For the present purpose, however, the table will give quite a sufficient picture of the temperature conditions.

The total length of the adult female increases during the summer and the biggest animals are found in autumn. The older and the fewer the population is, the bigger are the different individuals.

The discussion above indicates that the water temperature most probably does not start the formation of helmets, nor does it affect their size. On page 178, I have already pointed out the applicability of BROOKS' "turbulence theory". If, according to BROOKS, there is a direct effect of the water movements that starts the helmet formation, there must also be a physiological mechanism that responds to changes in the environmental conditions caused by the circulating water. The purpose of this response might very well agree with the stability theory of WOLTERECK, meaning that in the circulating water stabilizing organs have to be developed in order for the animals to retain their position in their relatively restricted food-layers of the epilimnion. This agreement between the two theories has been touched upon before by WOLF (1955). HRBÁČEK (1959) has also examined the effect of circulating water on the relative growth of *Daphnia*. His results agree well with those of BROOKS and provide further evidence for the "turbulence theory". HRBÁČEK concludes that the increased helmet size in *Daphnia* serves as stabilizers against the effect of currents. Though the necessity of stabilizing organs can not be considered as fully proved I have once more brought up this explanation for discussion, because in Ransaren no other hitherto published explanation seems to fit.

Finally I have to add that though the water temperature in Ransaren

seems to play a very subordinate rôle, I do not question that in other lakes other forms of *Daphnia* for their growth are more dependent on changes in temperature.

Summary

The populations of *Cyclops scutifer* and *Daphnia galeata* in two northern Swedish lakes have been studied. *Cyclops scutifer* appears in two different types that are morphologically alike but differ in their length and their annual cycle. They correspond closely to the two fractions of the species that have been described by LINDSTRÖM from other lakes in Northern Sweden. *Daphnia galeata* occurs in different seasonal forms, the *microcephala*, *obtusifrons* and *galeata* form. The first two types are round-headed and the last one is helmeted. The course of the cyclomorphosis may be connected with the turbulence of the water according to the experiments by BROOKS (1947) and HRBÁČEK (1959). The water temperature seems to play a subordinate rôle.

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The bottom fauna of natural and impounded lakes in northern Sweden (Ankarvattnet and Blåsjön)

By ULF GRIMÅS

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1. Introduction

The influence of lake regulation upon the bottom fauna has been studied since 1956 in the subarctic lake Blåsjön in northern Sweden. Comparisons have been carried out with the conditions known from this lake before the regulation (BRUNDIN 1949, MÄÄR [in manuscript]) and with the nearby lake Ankarvattnet which has not been regulated.

This investigation forms part of the program of the Institute of Freshwater Research, Drottningholm, aiming at the elucidation of the conditions of production in regulated Swedish lakes, and has been financed by grants from *Indalsälvens and Faxälvens Vattenregleringsföretag*, *Skandinaviska Elverk Aktiebolag*, and the *Migratory Fish Committee*. The analysis of the material has been carried out at the Entomological Department of the Zoological Institute at the University of Uppsala and the Museum of Natural History, Stockholm. The author is greatly indebted to the heads of the institutes mentioned, Professors Bertil Kullenberg and Lars Brundin and to Professor Sven Runnström, Director of the Institute of Freshwater Research, for their stimulating interest, generous help, and positive criticism.

Professor Olof Lundblad, Stockholm has kindly identified all the Hydracarina collected and Dr. Karl-Herman Forsslund the Trichoptera imagines. Dr. Lars Karlgren and Dr. Torsten Ahl have made all waterchemical analyses.



Lake Blåsjön. Section of the typical block zone in the upper littoral.

2. Material and methods

The investigations into the distribution and composition of the bottom fauna in Blåsjön have been concentrated first of all to 6 main sections. Of these, three are situated near the inflows, and correspond to the region examined by MÄÄR before the regulation. The remaining sections have been chosen so as to illustrate situations in bottoms which to the least extent are influenced by inflows. After a course of 3 km one section reaches the greatest depth of the lake, viz. 147 m. This spot has been selected as the main station for the continuous control of the chemistry of the water, the transparency, and the temperature zoning in the lake. The corresponding station for sampling in Ankarvattnet forms the end of the bottom section examined in the lake.

The measurements of the temperature in the water, altogether 32 series, and in bottoms affected by drainage have been carried out with thermistors (type Western Electric Comp., 14 B). The temperature of the air has been measured with selfregistering apparatus. Forty determinations of the transparency have been carried out with the Secci-disk. Altogether 54 samples of the water from the lakes and their feeders have been chemically analysed by L. KARLGREN and T. AHL at the Limnological Institute of the University of Uppsala.

The quantitative collecting of the material has been carried out with a bottom sampler, type EKMAN-BIRGE, and with hatching funnels, construction BRUNDIN (1949). This material comprises about 42.000 animals, obtained from 473 bottom samples, covering a total area of the bottom of 10.8 sq.m., and 369 hatching samples. The sifting of the bottom samples has been carried out with a sieve of 0.6 mesh, the sorting of the material under a binocular magnifier with 6 times magnification. Block bottoms covering a total area of 7.9 sq.m. has been controlled regarding to insect larvae.

The qualitative material comprises the benthonic organisms and the aquatic insects in the stages of hatching (=emergence), swarming, and deposition of eggs.

A common status of the water-level is an important basis for comparisons between different lakes. The seasonal variations are great, and are accentuated by the alterations caused by the regulation. It appears natural to base the analysis on the situation during the relatively stable water-level after the ebbing out of the spring flood, i.e. during the time which comprises the main period of production. Thus the starting point for the fixation of comparable depth zones has been the average level of the water during the summer which in the regulated lake amounts to the level near to the damming-up limit.

3. The lakes

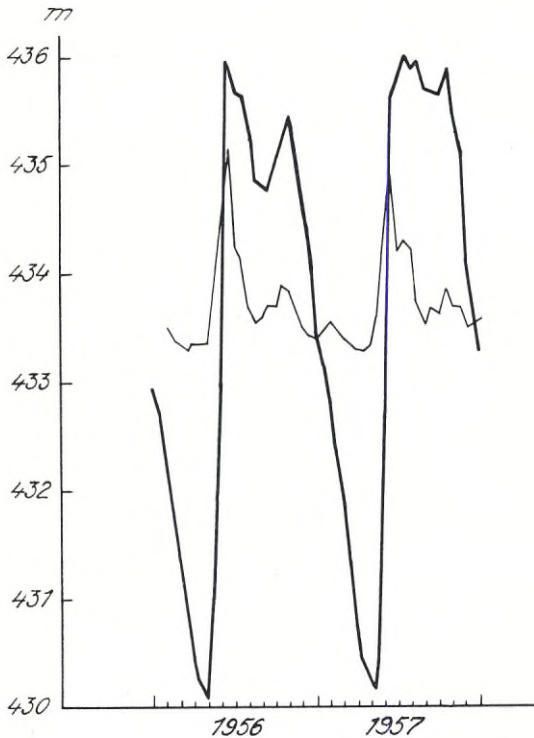
Both Blåsjön and Ankarvattnet are situated within the subarctic region of northern Jämtland at the altitude of 435 and 448 m., respectively. The distance between the lakes amounts to less than 3 km. The lakes are connected with each other by Ankarälven which forms the most important feeder of Blåsjön.

Blåsjön which covers a total area of 39.96 sq.km. can be divided into two parts, viz. St. and L. Blåsjön, which are connected by a rather narrow and shallow sound. The area of Ankarvattnet is 9.34 sq.km. Both lakes possess a well developed profundal. The greatest depth is 147 m in Blåsjön and 70 m in Ankarvattnet.

The basin of the lakes as well as their drainage area are situated upon the same bed-rock which is dominated by schists (ÄNGEBY 1947).

The above-mentioned factors contribute to the close agreement existing between the two lakes with regard to climate and the physico-chemical properties of the water. This again finds expression in far-reaching similarities with regard to fauna and flora between Ankarvattnet as known from this investigation and Blåsjön prior to regulation (BRUNDIN 1949, MÄÄR [in manuscript], QUENNERSTEDT 1959).

At the time of this investigation the regulation of lake Blåsjön had been in force for about 10 years, the annual amplitude of the water-level being



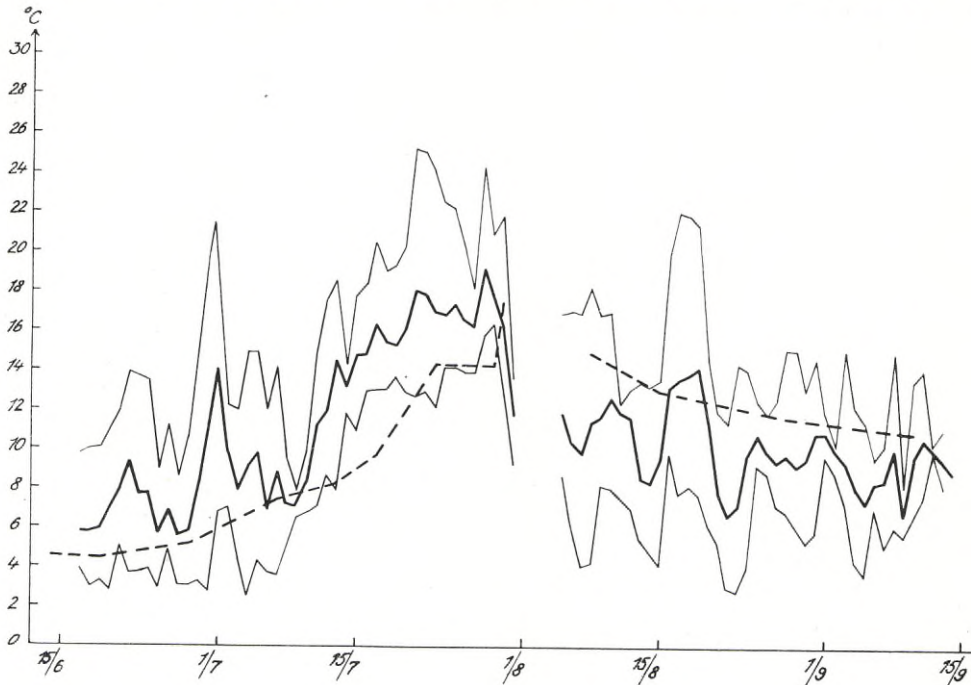
Diagr. 1. The water level fluctuations in Lake Blåsjön. Thick line = regulated water level, thin line = estimated unregulated water level.

6 metres. This amplitude is composed of a rise of 2 metres and a drop of 4 metres in relation to the normal water-level in summer before the regulation. The damming-up occurs in spring (May-June) followed by a relatively stable water-level at the damming-up limit during the summer. The definite lowering begins in October—November, and the water-level usually reaches the draw down limit in early spring, leaving large areas of the bottoms drained during the winter (Diagr. 1).

Both lakes can be characterised as oligotrophic and oligohumous with a high content of oxygen in the hypolimnion water throughout the year. On the basis of temperature zoning, transparency, and the limits for the distribution of aquatic vegetation and of the organisms typical for the profundal the transition zone between the littoral and the profundal has been calculated as lying at a depth of between 12 and 15 metres counted from normal summer water-level in both lakes.

Temperature conditions

There exist no detailed investigations about the effect of a regulation upon the temperature conditions in the free mass of the water. It can, however, be assumed that in Blåsjön the general annual course of temperature has not undergone any noticeable changes.



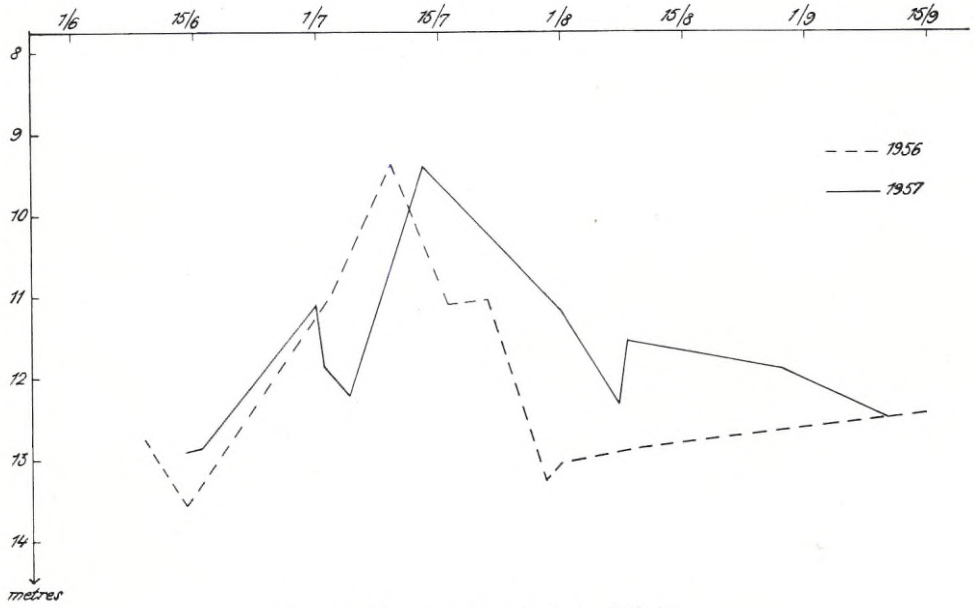
Diagr. 2. Temperature of air and water in Lake Blåsjön, 1957. Thick line=mean air temperature, broken line=temperature in the water surface.

During about four months, viz. between the middle of June and the middle of October, the temperature of the epilimnion exceeds 4°C . Only a thin layer at the surface extending to a depth of three metres shows temperatures higher than 15°C ., and then often only during a short period lasting about one week. During October the lakes become homothermous, and the total mass of water continues to cool down to temperatures sometimes below 4°C . prior to the appearance of the ice cover in December. Here it can be noticed that as a rule Ankarvattnet is covered with ice earlier than Blåsjön. The breaking-up of the ice generally occurs in either lake in the first days of June (Diagr. 2).

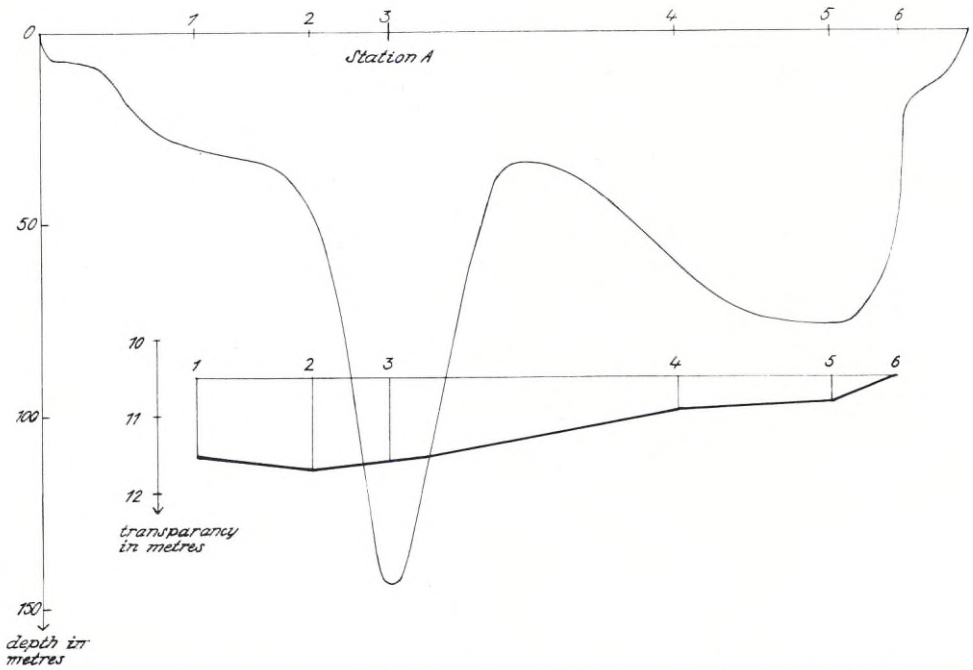
For the influence of the regulation upon the temperature conditions in the bottom sediments the reader is referred to p. 221 ff.

Transparency

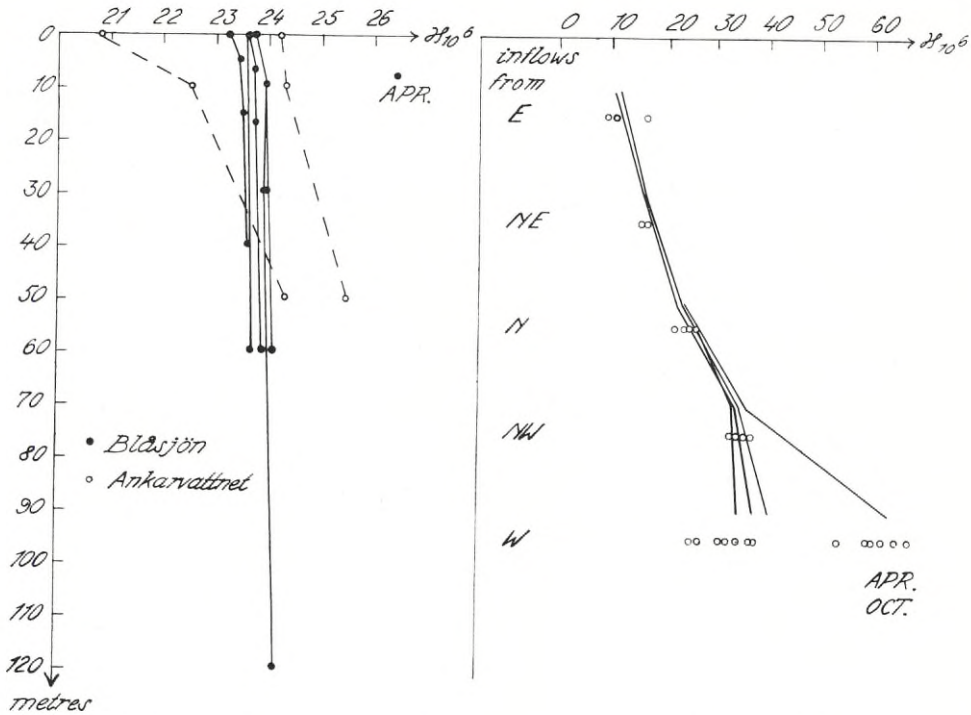
As an immediate consequence of the regulation the transparency of the water in Blåsjön ought to have undergone a strong decrease in the first years after the regulation, the reason being an intensive redeposition of the sediment from the regulated zone. After 10 years of regulation there exist no essential divergences from Ankarvattnet and Blåsjön before the regulation.



Diagr. 3. Transparency in Lake Blåsjön.



Diagr. 4. Section through Lake Blåsjön from west to east and the transparency conditions on Aug. 8, 1957.



Diagr. 5. The conductivity of water in Lakes Blåsjön and Ankarvattnet, and the important inflows of Lake Blåsjön.

During one year the transparency varies between the limits 9.5 and 13.5 metres (Station A). The penetration of the light is greatest in spring soon after the breaking-up of the ice, and smallest during the first half of July. The course of the curve (Diagr. 3). seems to be determined mainly by the autochthonous production of planktonic organisms. Divergences from these main conditions are found near inflows, where the quantity of allochthonous material supplied by the spring flood produces a minimum. Especially the influence of the two rivers Ankarälven and Lejaren is noticeable in this respect in the eastern part of Blåsjön, and even later in the year, as can be seen from the section through St. Blåsjön in August 1957 (Diagr. 4).

Chemical conditions

In Blåsjön the chemical conductivity ($\times 10^6$) varies between the observed values 23.2 and 26.4. With the exception of occasional divergences in spring, immediately before the breaking-up of the ice, which seem to depend upon the interstratification of water from the western inflows the annual variations in the content of electrolytes are small (Diagr. 5).

Table 1. Chemical data.

	Blåsjön		Ankarvattnet	
Conductivity, $H_{18} \cdot 10^6$	23.2	— 26.4	20.8	— 25.5
Alkalinity, $\mu\text{ekv/l}$	130	— 150	101	— 123
Ca + Mg, $\mu\text{mol/l}$	85.5	— 97.0	70.8	— 89.0
SO ₄ , mg/l.....	2.06	— 2.30	1.96	— 2.10
Cl, mg/l.....	1.96	— 2.12	2.26	— 2.65
Tot-P, $\mu\text{g/l}$	3.6	— 5.7	3.2	— 4.7
Tot-N, $\mu\text{g/l}$	83	— 113	72	— 112
Si, mg/l.....	0.612	— 0.627	0.521	— 0.571

Analyses for the different chemical components confirm the oligotrophic character of the lakes (Table 1). Variations which might be conditioned by changes accompanying regulation in Blåsjön do not seem to surpass the natural variations depending on seasons and depth zones.

Bottom conditions

According to the investigation carried out by MÄÄR in Blåsjön prior to the regulation the sediments in the first metre below the water-level seem to be dominated by blocks to sand. In less exposed situations the sand is mixed with finer particles. Already within a depth of two metres more fine-grained minerogenic sediments become increasingly common. The same applies to an addition of organogenic material derived, in part, from the aquatic vegetation. With a depth increasing by a few metres the percentage of sand in the sediment successively decreases.

In regions near the inflows which have been the special objects of MÄÄR's faunistic investigations the bottom regions which are dominated by sand extend as a rule towards greater depth.

The bottom conditions in Ankarvattnet and other comparable lakes agree with those in Blåsjön before the regulation. The occurrence of organogenic sediments can also be observed already in the topmost one-metre zone.

In the littoral of the regulated Blåsjön the composition of the bottom sediments is different.

The uppermost two metres which comprise the area submerged by the damming-up, and which amount to 18 per cent of the entire regulated area slope rather steeply. This zone is characterized by block bottom interspersed with gravel. Only small sectors, altogether about 1 % of the whole shore line and protected against erosion, preserve their previous nature of mire or wooded ground. Bottoms outside cultivated ground (about 7 per cent of shore line), are temporarily powdered by finer sediments derived from eroded land after high wind.

The remaining 82 per cent of the regulated area constitute old lake bottom.



Lake Blåsjön. Eroded land above the damming-up limit.

Between 2—5 metres' depth the sediments are dominated by sand. Smaller particles might occur especially outside cultivated land, but then always compose thin isolated "islands", these particles being continuously transported to areas below the draw down limit. Off inflows similar "islands" are formed by outdrifted detritus.

Between 5 and 6 metres' depth the sand still predominates, but is here mixed homogeneously with particles of smaller size. These particles are foliated if not completely comminuted, and originate from the easily decomposed schists.

Below the draw down limit at 6 metres the true fine sediments begin. As also shown by MÄÄR the sediments are rich in iron which forms a crust, covering large areas of the profundal region. The crust is overlain by "gyttja" of variable thickness.

The littoral regions below the draw down limit have, however, received great quantities of eroded material, mainly of minerogenic origin, which have been deposited on top of the original sediments, and have altered the character of the bottoms. This off-shore transport of eroded material affects also deeper regions of the profundal. When this happens, the organogenic contact limit of these bottoms towards the water becomes covered up or punctuated (see p. 227 ff).

As a summary it can be established that the factors which have governed the development in Blåsjön seem to have acted towards a transformation of the environment in which development has not been noticeably influenced by modifying factors. As examples we can mention that the annual rhythm of regulation has not undergone any essential changes, and that all bottom regions within comparable depths have been uniformly influenced by the eroding agencies right around the lake. Only relatively coarse minerogenic material is retained within the zone of regulation.

The aquatic vegetation

In Ankarvattnet the aquatic vegetation is entirely dominated by submersed carpets of vegetation (QUENNERSTEDT 1959), composed mainly of *Isoetes lacustris*. In the shape of small individuals *Isoetes* appears already within the uppermost metres below the surface, and extends down to 6 metres, with a greatest abundance between 2 and 5 metres. Identical conditions are described for Blåsjön before the regulation. The great vertical amplitude in both lakes is worthy of particular notice. The same applies to the quantitatively important great alga *Nitella opaca* which, however, descends throughout to greater depths than *Isoetes*. Among the remaining vegetation in Ankarvattnet and in Blåsjön before the regulation we can mention *Ranunculus peltatus* and *R. reptans*, *Myriophyllum alterniflorum*, *Potamogeton gramineus*, *Sparaganium* sp. and, especially in the first metre below the surface, *Eleocharis acicularis* and *Subularia aquatica*. Clusters of plants emerging above the water, especially *Equisetum fluviatile*, are found in protected coves only.

The regulation of Blåsjön has caused a complete elimination of macrophytes within in the regulated zone which can be attributed mainly to the freezing of the bottom in winter. The rise of the water-level and the long duration of a high water-level during the productive summer period in comparison with natural lakes produces furthermore an upward shifting of the original lower distribution limit of the vegetation (QUENNERSTEDT 1958).

After the regulation the submersed carpets of *Isoetes lacustris* are no longer found in Blåsjön, and of larger plants only some sparse stands of the great alga *Nitella opaca* are found immediately below the draw down limit.

QUENNERSTEDT's investigations demonstrate great changes also in the micro-vegetation. In Blåsjön not even fast spreading species are able to grow into visible fluff, and there exists no resemblance to the closed permanent micro-vegetation of the littoral region in Ankarvattnet.

Table 2. Bathymetrical distribution of bottom animals in Lakes Blåsjön and Ankarvattnet: individuals/m².

Depth zone	Blåsjön	Ankarvattnet
0— 2 metres	938	9,652
2— 4	1,550	7,882
4— 5	2,017	5,497
5— 6	3,187	—
6— 7	5,275	4,596
7— 8	4,755	—
8— 10	4,090	4,444
10— 13	2,905	3,708
13— 20	1,474	2,717
20— 30	750	1,599
30— 70	717	1,243
70—140	884	—

4. The bottom fauna

The regulation of Blåsjön has resulted in a reduction of the entire bottom fauna which can be estimated at 70 per cent in the regulated zone and at 25 per cent in the remaining areas.

The distribution of the bottom fauna in the depth zones of the two lakes can be seen from Table 2 which forms the basis of the adjoined Diagram 6.

The diagram indicates the density of individuals per sq.m, and comprises Insecta, Crustacea, Hydracarina, Mollusca, Oligochaeta, Hirudinea, Turbellaria, Nematoda, and Hydrozoa. Small individuals of which an appreciable percentage can be expected to be lost in sifting have been excluded. This remark applies to the smallest species of Cladocera, Oligochaeta, and Nematoda and to newly hatched larvae of Chironomidae.

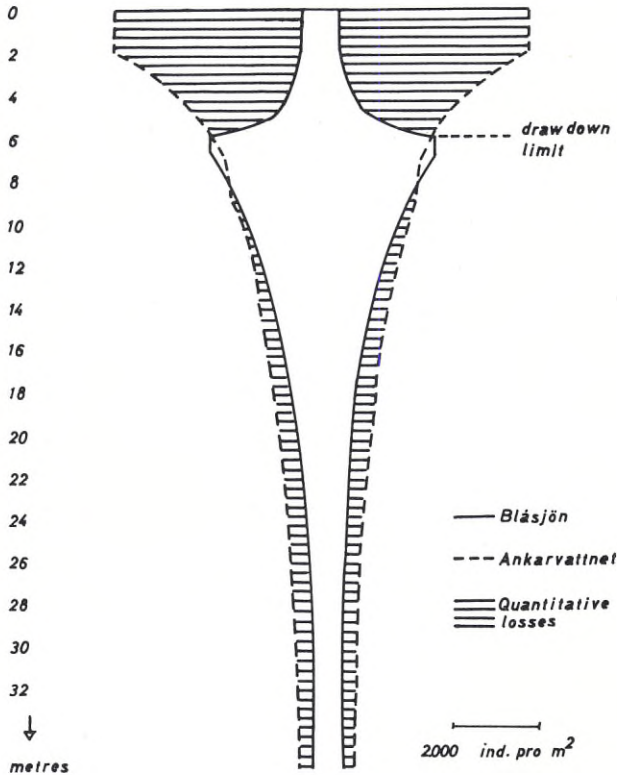
The distribution of the fauna in Ankarvattnet can be considered representative for the conditions in unregulated lakes within the region. The greatest abundance is found in the topmost two metre-zone of the littoral. Farther down the density of individuals diminishes rapidly towards relatively uniform values in the greater part of the profundal.

In the bottoms of Blåsjön the greatest abundance of the entire fauna is found in depth zone 6—7 m, i.e. immediately below the draw down limit.

Compared with the corresponding regions in Ankarvattnet the distribution curve is inverted in the regulated zone, and the most important faunal region of Blåsjön, within the upper littoral, can be considered as almost eliminated.

An abundance comparable with that in Ankarvattnet is reached in Blåsjön only in a narrow depth zone below the draw down limit. Towards deeper regions losses are again noticeable.

The diagram has been worked out on the basis of all the bottom samples taken, and thus shows the annual average distribution in the two lakes. The



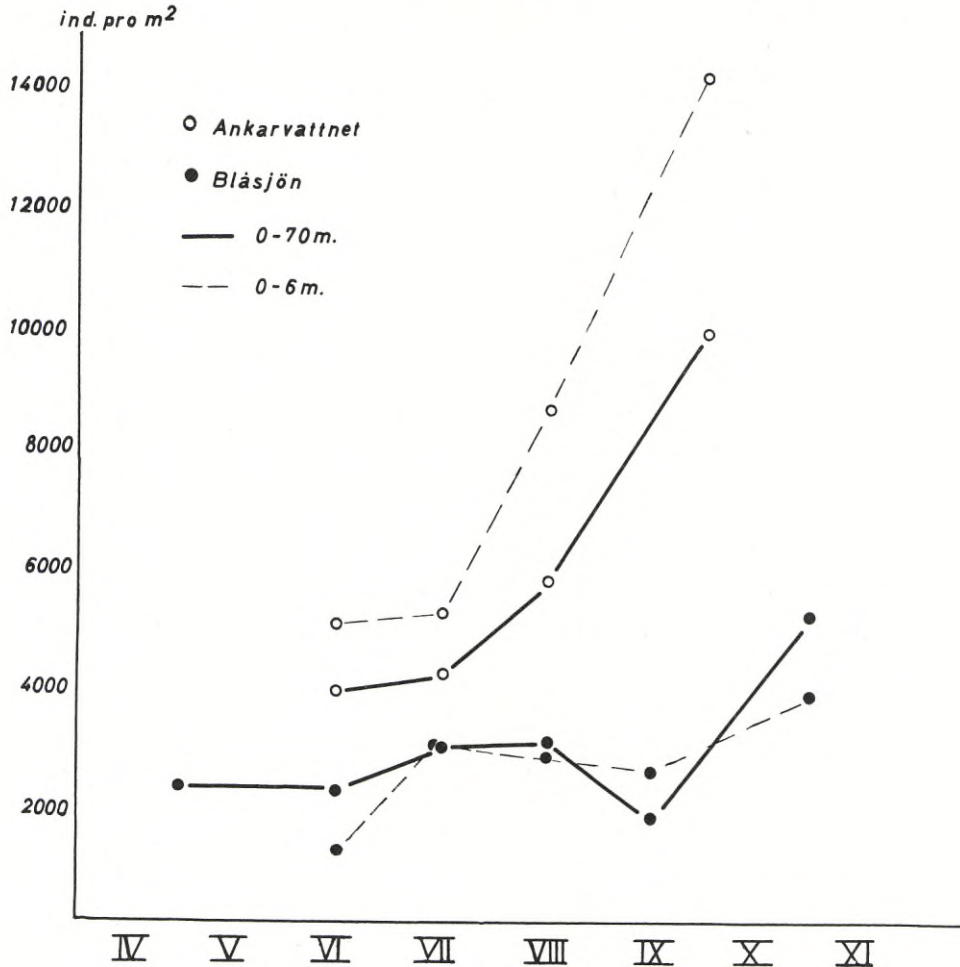
Diagr. 6. The bathymetrical distribution of the bottom fauna in Lakes Blåsjön and Ankarvattnet.

density of individuals is, however, subject to seasonal variations, and as a general rule it can be said that the entire fauna has a small density in spring and a great one in late autumn, especially within the littoral (Diagr. 7). The diagram also shows the gradual increase of the differences between the two lakes in the course of the summer, the maximum difference being reached in autumn.

As a general rule it can also be laid down that in Blåsjön the greatest abundance is found near the inflows.

Special conditions exist in the pronounced block bottoms. A fauna specific for this zone and resembling that in Ankarvattnet is lacking in Blåsjön, where only the regions in the immediate vicinity of the inflows are populated mainly by floated-in organisms from the running water.

Certain changes have occurred regarding to the balance between the various animal groups (Table 3). Most notable is the increased relative share of *Chironomidae* (cf. CUERRIER 1954, RAWSON 1958, MILLER and PAETZ 1959). After the regulation the chironomids extend to 54.1 per cent of the entire bottom fauna, while available material from Blåsjön before the regulation (MÄÄR, unpublished) shows a value of 31.9 per cent. Similar conditions



Diagr. 7. Seasonal changes in the abundance of the entire bottom fauna in Lakes Blåsjön and Ankarvattnet.

prevail in other unregulated lakes within the region. The material from Ankarvattnet shows 32.2 per cent and MÄÄR reports for lake Jomsjön 29.7, Kvarnbergsvattnet 36.1, and Semningsjön 35.2 per cent.

No other animal group shows a relative increase comparable with the chironomids. The *Oligochaeta*, for example, amount to 12.8 per cent in Ankarvattnet and 13.1 per cent in Blåsjön after regulation. The losses in the regulated area are compensated by a higher abundance below the draw down limit.

Several animal groups show a relative decrease. The *Cladocera* in connection with bottom sediments amount to 24.3 per cent in Ankarvattnet and

Table 3. Main groups of animals calculated as percentages of the entire fauna.

	Blåsjön	Ankarvattnet
<i>Chironomidae</i>	54.11	31.91
<i>Cladocera</i>	14.20	24.26
<i>Oligochaeta</i>	13.13	12.79
<i>Pisidae</i>	6.04	5.51
<i>Nematoda</i>	4.03	3.13
<i>Copepoda</i>	3.20	3.72
<i>Hydracarina</i>	1.87	0.62
<i>Turbellaria</i>	1.05	1.03
<i>Hydrozoa</i>	0.63	9.20
<i>Insecta/excl. Chir./</i>	0.57	2.36
<i>Gastropoda</i>	0.52	0.92
<i>Ostracoda</i>	0.44	0.23
<i>Gammarus lacustris</i>	0.20	4.28
<i>Hirudinea</i>	0.01	0.04
	100.00 %	100.00 %

14.2 per cent in Blåsjön after regulation, and the losses appear mainly in the littoral. Typical littoral forms as *Gammarus lacustris* and many insect larvae decrease to a great extent.

Insecta

Chironomidae

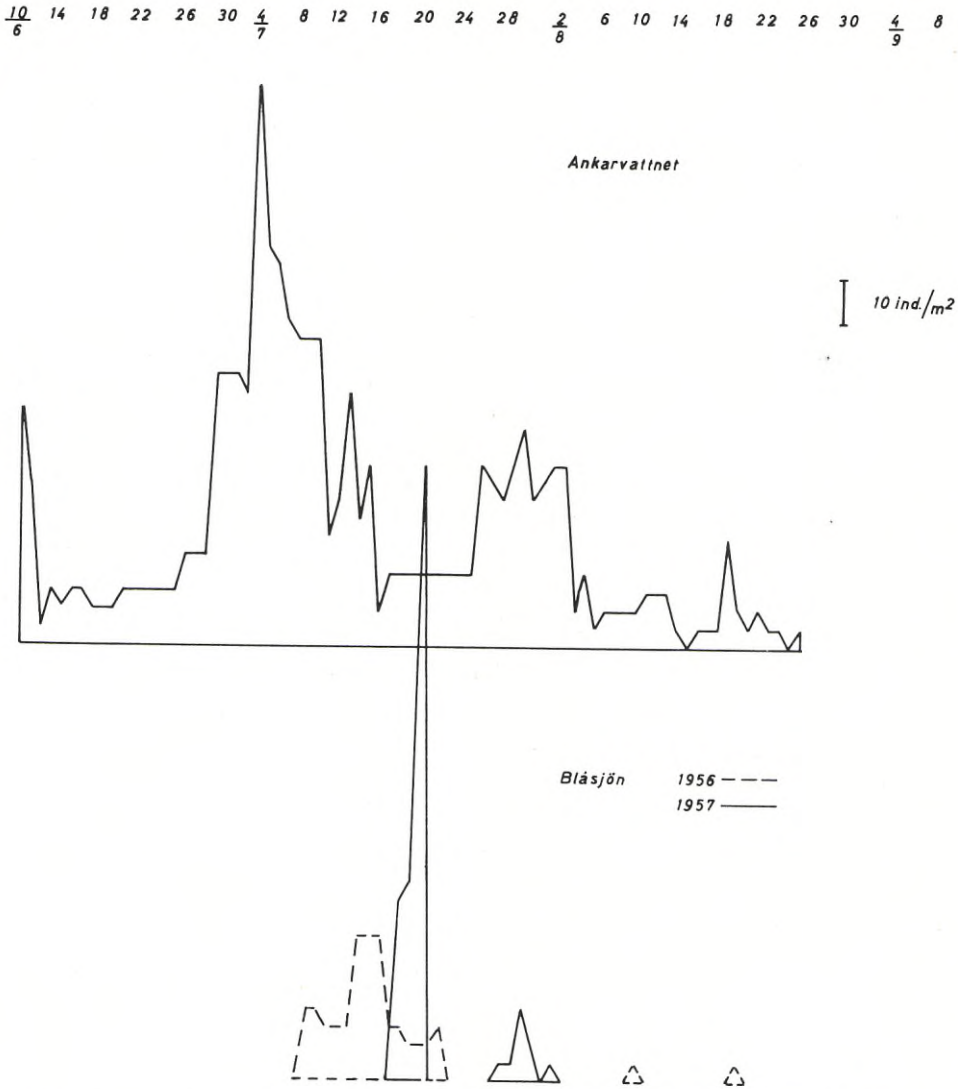
Phenology

In all the examined regions of the littoral the hatching in Ankarvattnet is divided into four periods. Hatching in spring, early summer, midsummer, and late summer are distinguished. The results do not differ from those reported by BRUNDIN from Blåsjön before the regulation or from the conditions known from other sub-arctic lakes (THIENEMANN 1941).

The regulation has caused great changes in Blåsjön, the spring hatching having been eliminated in the entire littoral, thus also in the regions which are not directly affected by the lowering of the water-level.

Within the upper littoral only one of the four natural periods is still in existence (Diagr. 8). This can be designated as a retarded early summer hatching. Towards the middle and lower littoral in addition also midsummer and late summer hatching occur (Diagr. 9). Furthermore a time lag is universal among the species present, and more marked in species with a natural orientation towards the upper littoral.

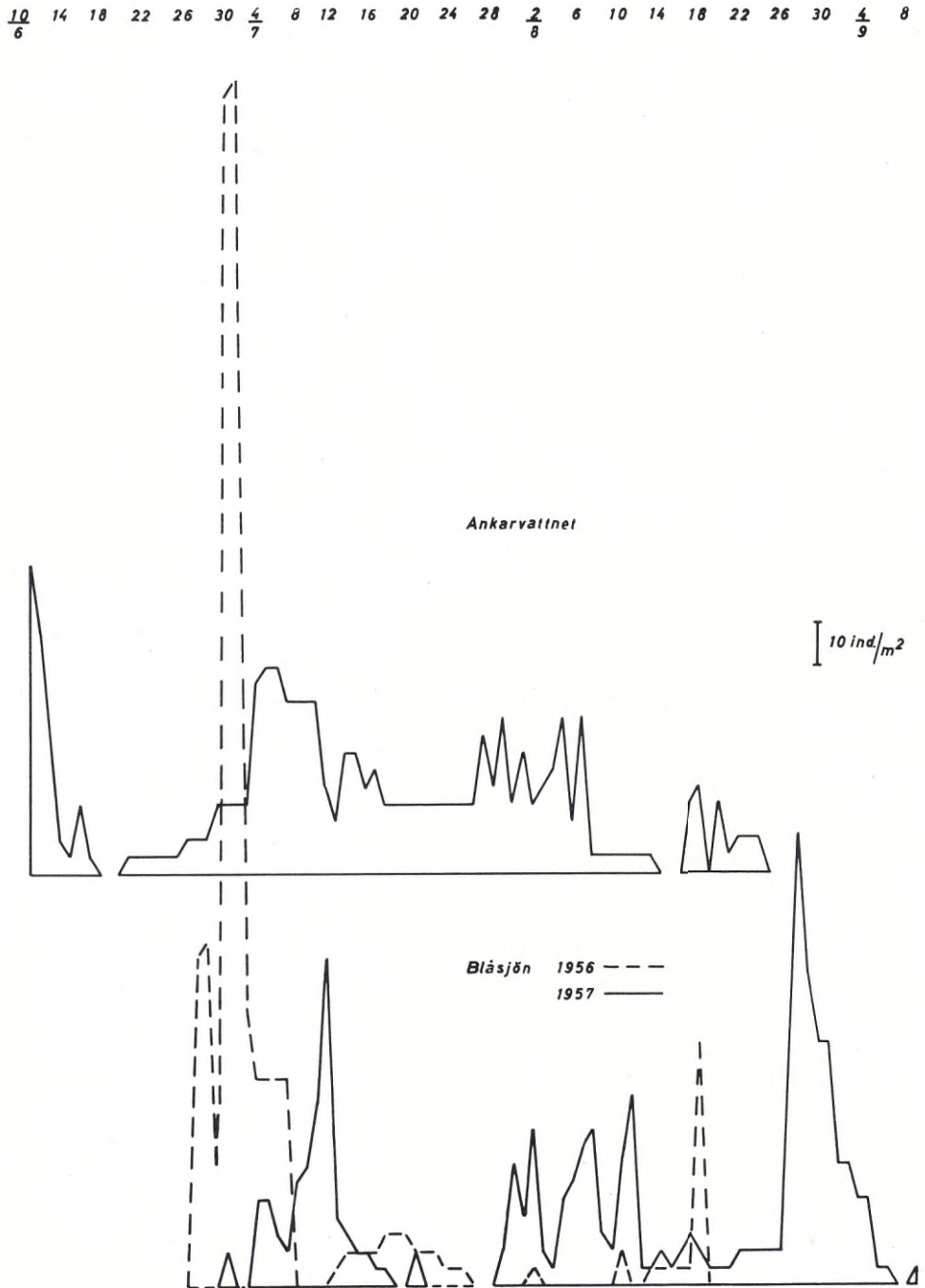
A comparison of the phenological with the bathymetric and qualitative results obtained in Ankarvattnet exposes a tendency towards a connection between the seasons and the centres of hatching in the lake (Diagram 10). The distribution expressed as percentages of species and individuals among the different depth zones shows a dominance of the profundal region during



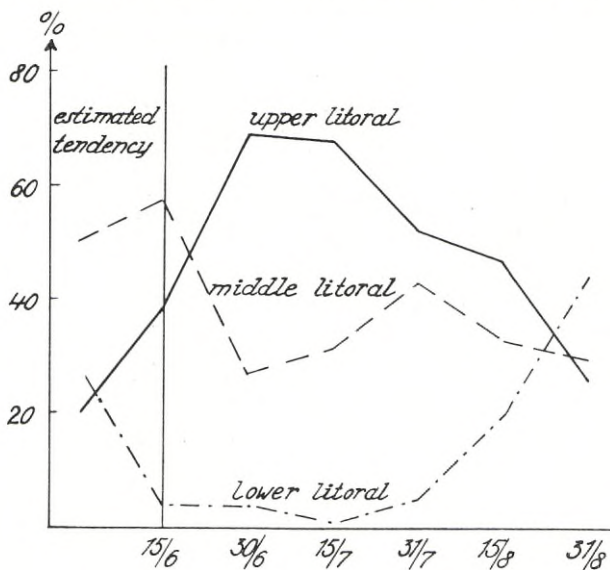
Diagr. 8. Seasonal changes in the hatching of Chironomidae in Lakes Blåsjön and Ankarvattnet. Depth zone 2—4 metres.

the very early spring. While spring gives way to early summer the centre of gravity shifts over the middle towards the upper littoral. Afterwards, towards late summer, the centre of hatching shifts again towards the deeper regions.

In Blåsjön the seasonal occurrence in the various depth zones of hatching periods does not differ in principle from those in Ankarvattnet. The central summer hatching in the upper littoral is framed in by species from the middle



Diagr. 9. Seasonal changes in the hatching of Chironomidae in Lakes Blåsjön and Ankarvattnet. Depth zone 5—6 metres.



Diagr. 10. The hatching of Chironomidae in the littoral Zone of Lake Ankarvattnet, showing the distribution in per cent of individuals in different depth zones during different seasons.

littoral, and towards extreme spring and late summer from the lower littoral and the profundal. The fact that this phenomenon is more distinct in Blåsjön can be attributed first of all to a general reduction in the number of species.

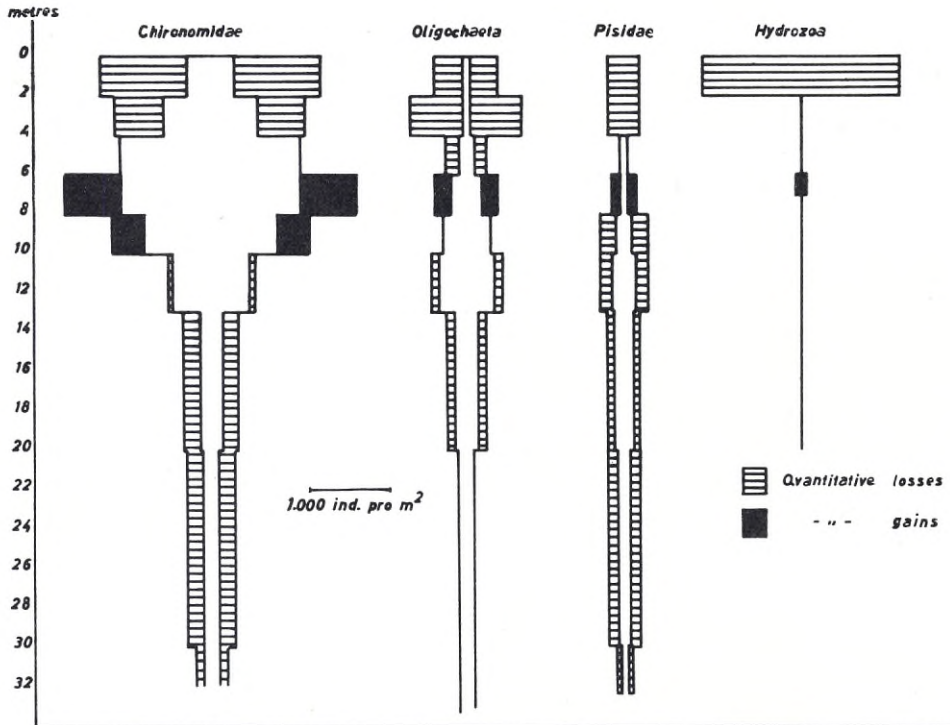
Bathymetric conditions

Of the 18 species which show an abundance maximum in the upper littoral of Ankarvattnet only one, *Parakiefferiella bathophila*, is left in Blåsjön after the regulation. All the others have either been eliminated or shifted in small numbers towards deeper zones in the lake.

A universal feature in Ankarvattnet is the occurrence of the species within wide bathymetric limits. In Blåsjön only *Constempellina brevicosta* appears in all the examined zones of the littoral. In this lake every depth zone seems in principle to be occupied by some few species among which one can be designated as the "specialist" of its zone with a tendency towards stenobathic distribution, e.g. *Paratanytarsus hyperboreus* and *Psectrocladius fennicus*.

Table 4. The total number of hatching chironomids during the experiments in Lakes Blåsjön and Ankarvattnet.

Depth zone	2-4	5-6	7-8	8-10	10-13	13-20	total	investigation period
Blåsjön 1956	58	304	61	26	28	24	501	68 days
Blåsjön 1957	65	288	148	24	37	26	588	83 days
Ankarvattnet	485	309	—	—	71	—	865	78 days

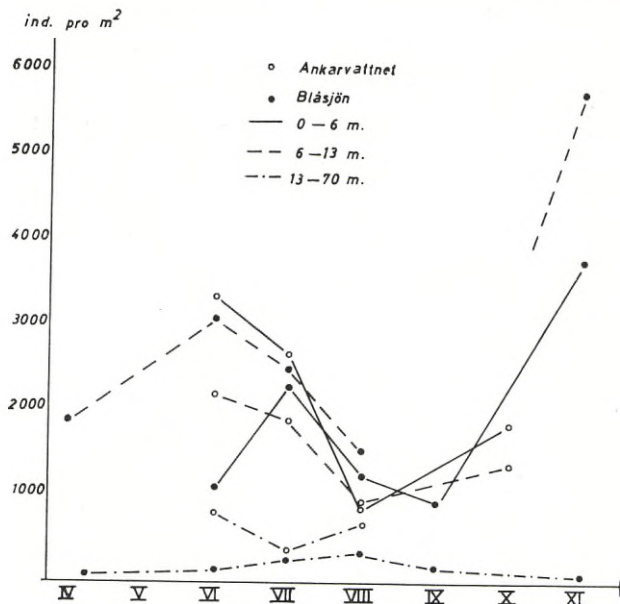


Diagr. 11. The bathymetrical distribution of some bottom animals, showing losses and gains in quantity in Lake Blåsjön.

Quantity

The quantitative distribution of the hatching material from the littoral of Ankarvattnet shows complete agreement with the known distribution of the bottom fauna. The intensity of hatching is greatest in the upper littoral, and diminishes towards deeper regions (Table 4). In Blåsjön the region in close neighbourhood of the draw down limit exhibits the greatest number of hatching individuals (Table 4), viz. 73 and 74 % in 1956 and 1957, respectively. This region is, however, characterized by unstable conditions in the sense that a dominant spring species can be replaced as dominant in the following year by one that hatches in late summer. With increasing distance from the draw down limit the different species are found to contribute to the hatching in a less changing way. The sensitivity evinced by the species in close connection with the draw down limit can be traced back to the course of the regulation which varies between different years.

The calculation of the quantitative losses in Blåsjön shows different results for larvae and hatching chironomids. The difference between Ankarvattnet and Blåsjön concerning the abundance of larvae is not remarkable



Diagr. 12. The seasonal changes in the abundance of Chironomidae in Lakes Blåsjön and Ankarvattnet.

(Diagr. 11) which depends on the high density of larvae, mainly Tanytarsini, in the bottoms of Blåsjön during November (Diagr. 12), a month which is not covered by samplings in Ankarvattnet. A comparison between the supply in November and the situation one month after damming-up in Blåsjön shows, however, a reduction of 100 per cent in the depth zone 0—2 metres, 96 per cent in 2—4, 94 per cent in 4—5 and 76 per cent in the depth zone 5—6 metres. As can be seen from Table 5 the quantitative loss of hatching chironomids in Blåsjön is greatest in the upper littoral, and can be estimated at 75 % for the entire littoral. In this calculation the results of the examination of the bottom fauna are also included, covering that part of the spring hatching which is not covered by the hatching experiments in Ankarvattnet.

Quality

The results are collected in the tables 16 and 17. With regard to quality the results obtained in Ankarvattnet agree with generally known conditions. The upper littoral is the region richest in species. This is due to the

Table 5. The quantity of hatching chironomids/day in comparable depth zones in Lakes Blåsjön and Ankarvattnet.

Depth zone	2—4	5—6	10—13	total
Blåsjön 1956, 1957	0.88	3.47	0.37	4.73
Ankarvattnet	6.22	3.96	0.91	11.09
Quantitative losses in Blåsjön, % ...	85.9	12.4	59.3	57.4

Table 6. The number of chironomid species of the different depth zones in Lakes Blåsjön and Ankarvattnet.

Depth zone, m	0—2	2—4	4—5	5—6	6—7	7—8	8—10	10—13	13—20	20—30	30—70	70—140
Hatching in Lake Blåsjön	—	4	—	10	—	20	12	11	4	—	—	—
Benthos in Lake Blåsjön	3	3	3	12	18	19	17	14	8	2	3	3
Hatching in Lake Ankarvattnet.....	—	44	—	38	—	—	—	14	—	—	—	—
Qualitative losses, in Lake Blåsjön, %	—	91	—	74	—	—	—	21	—	—	—	—

widely varying environmental conditions of the region and a richly faceted system within the biocoenosis. Agreement exists also with regard to the distribution and maxima of species during the summer (THIENEMANN 1941, BRUNDIN 1949).

In Blåsjön the regulation has resulted in heavy qualitative losses. Table 6 shows the existence of a constant low number of species as far down as 1 m above the draw down limit. The deficiency extends also further down to regions below this limit. For the regulated part of the littoral the qualitative losses can be calculated at 80 per cent. For the entire littoral they are estimated at 60 per cent. This reduction in the number of species is most marked during spring and early summer.

The balance between the four represented main groups of the *Chironomidae* undergoes important changes.

In a discussion of the balance between the species and its dependence upon the geographical situation of the lake Ankarvattnet fits well into the system presented by BRUNDIN (1949). Apart from the great trends of development as one goes from the south-Swedish highland via high boreal and sub-arctic to arctic lakes BRUNDIN finds within the limited region of lakes in northern Jämtland a distinct change in the balance of species with increasing altitude. Most

Table 7. The balance between the main groups of *Chironomidae* in different subarctic lakes within the region. (Lakes Semmingsjön, Lebbikvattnet, and Blåsjön before the regulation. From BRUNDIN, 1949.)

	Blåsjön after regulation	Semmingsjön	Lebbikvattnet	Ankarvattnet	Blåsjön before regulation
<i>Tanypodinae</i> , %	11	14	12	12	19
<i>Orthoclaadiinae</i> , %	52	48	39	45	36
<i>Chironomini</i> , %	4	17	22	23	24
<i>Tanytarsini</i> , %	33	21	27	20	21
Number of species	27	42	51	56	85
Metres above sea-level ...	435	689	468	448	433

Table 8. The percentages of the four main groups of *Chironomidae* in the different depth zones of Lake Ankarvattnet. (Hatching results.)

Depth zone, m	2—4	5—6	10—13	Total
<i>Tanypodinae</i> , %	9	13	14	12
<i>Orthoclaadiinae</i> , %	55	45	43	45
<i>Chironomini</i> , %	16	21	29	23
<i>Tanytarsini</i> , %	20	21	14	20
Number of species	44	38	14	56

characteristic in this connection are the decreasing number of species, the increasing predominance of the *Orthoclaadiinae*, and the decreasing percentage of the *Chironomini* towards extrem sub-arctic lakes (Table 7). (The results from Ankarvattnet include only littoral species. This explains, amongst others, the sharply pronounced predominance of the *Orthoclaadiinae*.)

An analysis of the balance between the main groups with regard to the bathymetric distribution within the lake reveals an orientation of the *Orthoclaadiinae* towards the upper littoral, and increasing percentage of the *Chironomini* in the deeper areas within the lake, and an affinity of the *Tanytarsini* to shallower regions (see Table 8).

Thus if one compares on the one side the bathymetrical distribution of the main chironomid groups in the lake Ankarvattnet with the occurrence of these groups in lakes of different altitudes on the other, the environmental requirements of these chironomid types are reflected in an interesting way.

The conditions outlined above for natural environments can be said to be accentuated in regulated lakes. Table 7 shows that the number of species in all the main groups is reduced in Blåsjön. The relative magnitude of the different main groups shows, however, an increase in the percentages of the *Orthoclaadiinae* and the *Tanytarsini*, and a very marked decrease in that of the main group *Chironomini*.

From the bathymetric point of view the entire littoral of Blåsjön is dominated by the *Orthoclaadiinae* and the *Tanytarsini*. All the main groups are represented in only one depth-zone, and within the regulated region the *Tanypodinae* are altogether eliminated (Table 9).

Table 9. The percentages of the four main groups of *Chironomidae* in the different depth zones of Lake Blåsjön. (Hatching results.)

Depth zone, m	2—4	5—6	7—8	8—10	10—13	13—20	Total
<i>Tanypodinae</i> , %	—	—	15	8	18	—	11
<i>Orthoclaadiinae</i> , %	50	40	45	58	55	50	52
<i>Chironomini</i> , %	—	10	5	—	—	—	4
<i>Tanytarsini</i> , %	50	50	35	34	27	50	33
Number of species	4	10	20	12	11	4	27

Summing up we can state that the changes in the balance between the chironomid species and the reduction in the number of species which can be traced within the sub-arctic region with increasing altitude and with the climatic changes connected with it find their final expression in the regulated lake. Before the regulation the chironomid fauna of Blåsjön supplies an example of the conditions at the lower limit of the sub-arctic region. After the regulation the fauna is more extreme than that of lakes on the limit towards the arctic region on account of 1) the great reduction of the number of species, 2) the altered equilibrium between the species, and 3) the far-gone development of the tendencies concerning the bathymetric orientation of the groups.

From a wider point of view the tendencies concerning the position of the *Chironomini* in the fauna as one goes from the South-Swedish highland to the arctic region seem likewise to be fulfilled. Within this group one species only, *Paracladopelma obscura*, is left in Blåsjön.

Some remarks about the reaction of individual species to the regulation

With regard to their abundance before and after the regulation the chironomid fauna can be split into three groups.

1. Species especially favoured by the regulation.
2. Species which on the whole retain their position.
3. Species the abundance of which decreases or which are altogether eliminated by the regulation.

To group (1) belong first of all *Constempellina brevicosta* and *Abiskomyia virgo*.

These two species occur in the littoral of Ankarvattnet in an abundance corresponding to about 1 per cent of the fauna. For each of the species BRUNDIN reports less than 1 per cent in the bottoms of Blåsjön before the regulation.

Ten years after the regulation of Blåsjön *Constempellina brevicosta* forms 6 per cent of the hatching chironomids in the littoral. More striking is its higher percentage, viz. 15 per cent, in the larval material. The same increase in abundance applies also to *Abiskomyia virgo*. This species occupies mainly the regions close to the inlets of the lake, and there forms 16 per cent of the chironomid fauna. This increase finds no expression in the hatching experiments, since the hatching stations have intentionally been placed so as to represent regions that are influenced by the inlets as little as possible.

It is difficult to express an opinion about the causes of the increase in abundance of these two species without having a closer insight into their autecology. It can, however, be stated that they are favoured by the altered environmental conditions and the resulting disturbance of the balance be-

tween the species. Remarkable is the similar structure of the tubes in combination with a great movability of the larvae. These larvae are also independent of the surfaces of fine-grained sediments which are desirable for the majority of *Chironomidae*. This circumstance permits the colonization of the surfaces of the regulated area which are covered by coarse minerogenic sediments.

Among the species that on the whole retain their position after the regulation we remark such as are of great quantitative importance in unregulated sub-arctic lakes. After the regulation many of these species accentuate their original dominant position, but developing into what has above been called "specialists" squeezed into narrower depth zones. It is characteristic also that group (2) comprises only species of the main groups *Orthoclaadiinae* and *Tanytarsini*: *Parakiefferiella bathophila*, *Psectrocladius fennicus*, *Acricotopus Thienemanni*, *Cricotopus alpicola*, *Heterotrissocladus grimshawi*, and *Tanytarsus gregarius*, *Paratanytarsus hyperboreus* and *P. penicillatus*, *Microspectra groenlandica*. Altogether these species form a high percentage of the entire chironomid fauna, and account, together with *Constempellina* and *Abiskomyia*, for well over 95 per cent of the hatching in the zone of regulation and 80 per cent in the remaining littoral.

An important species is *Heterotrissocladus subpilosus* which before the regulation occurred in Blåsjön in such abundance that it was found appropriate to speak about a *Heterotrissocladus* lake (BRUNDIN 1949). It is decidedly a species of the profundal, but occurred also up to the lower parts of the littoral region in such abundance of individuals that it came to dominate the littoral fauna also. After the regulation it is no longer found in the littoral zone. Its quantitative importance has decreased also in the upper profundal, the species having to a large extent been replaced by *Microspectra groenlandica*. Thus the upper limit for the dominance of *Heterotrissocladus subpilosus* has been lowered from 10 metres to 20 metres in spite of the fact that the species is affected by neither drying up nor freezing in.

Other Diptera

Empididae, represented mainly by the genera *Haemerodromia* and *Atalanta*, are encountered in the littoral of the two lakes, with a distinct orientation towards its upper parts. In Ankarvattnet the greatest abundance, viz. 41 individuals per sq.m., is found at the depth of 0—2 m. Farther down the density of individuals decreases continuously with increasing depth. In Blåsjön the *Empididae* are entirely missing within this zone, but starting from the 2—4 metre-zone their distribution in the bottoms agrees with that in Ankarvattnet. The well delimited hatching period coincides for lakes as well as for species, and falls into the first half of August.

Tipulidae are sparsely represented in the material from either lake. Under

unregulated conditions the larvae are found almost exclusively in the upper littoral. Thus larvae of *Tipula* belong to this zone not only in Blåsjön before regulation but also in Ankarvattnet and lakes comparable with it, e.g. Kultsjön. They are, however, missing in the quantitative material from Ankarvattnet.

After the regulation of Blåsjön larvae of *Tipula* are found all over the region which is drained during winter, i.e. down to a depth of 6 m below the water-level of summer. It can be said that the regulation has brought about an increase of the areas suitable for the semi-aquatic larvae and pupae. This ought to imply an increase of the total number of *Tipulidae* in and near the lake.

The finds of larvae derive mainly from the wintery half of the year, and the generations seem to be ready for hatching during spring. In Blåsjön the larvae hibernate within limited regions to which they are concentrated. They are often found within regions that have been drained before the surface of the lake was covered with ice, and that are characterized by thin slabs of schists isolating a layer of fine sediment in which the larvae are embedded.

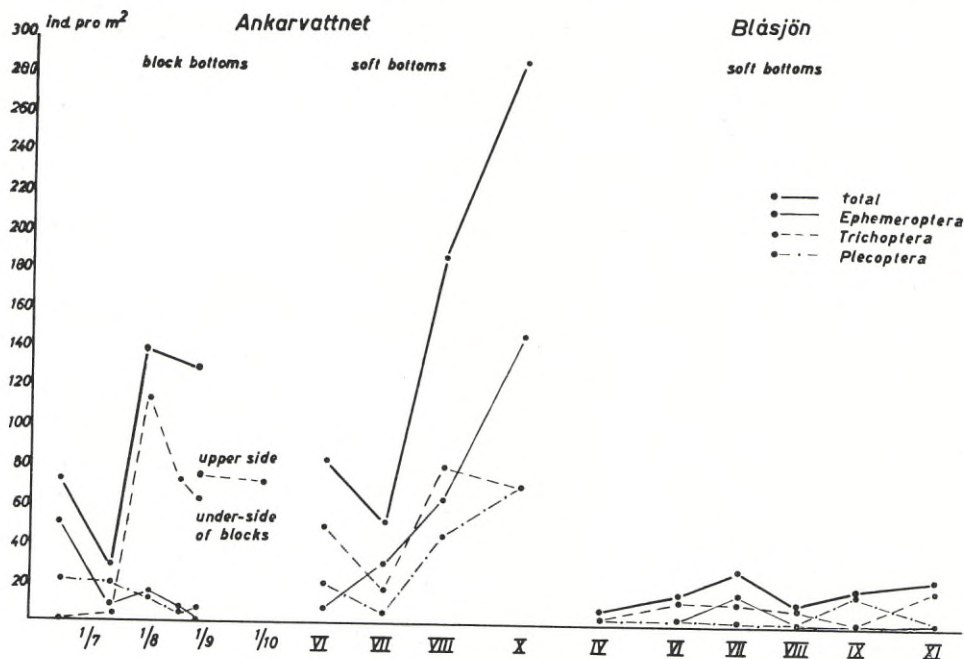
Imagines appear in and near the surface of Blåsjön most abundantly in the course of two periods, viz. the latter half of July and the beginning of September.

In addition to the *Diptera* treated above, which appear at the surface of the water in connection with hatching and oviposition, also terrestrial species occur that seem to be of importance as food for the fish. Especially noteworthy is the rich yearly occurrence at the surface of the water of *Lycoridae* at the shifting of June into July. Here we can also mention the dense swarms of imagines of *Hilaria* (*Empididae*) appearing during July and August along the shores of the lakes close to the surface of the water.

Large-sized larvae of insects

The larvae of insects, belonging to *Ephemeroptera*, *Trichoptera*, *Plecoptera*, and *Megaloptera*, are restricted to the littoral region. From among these the *Megaloptera* are entirely missing in Blåsjön, but are represented in Ankarvattnet by one species, *Sialis lutaria*, which occurs, however, sparsely in the quantitative material. The abundance of the other larvae is very low in Blåsjön as the result of the regulation and in part also a result of a new colonization of the bottoms within the regions of inflow, where the abundance is generally higher than in other bottoms.

In the littoral of Ankarvattnet we find a decreasing abundance during the early summer, with a minimum value in July. Subsequently, resulting from the new generations, the number of individuals increases to maximum values during the autumn. The universally small number of individuals in Blåsjön renders a more detailed analysis of the variations rather difficult, but the material indicates nevertheless a lowest density of the population in spring,



Diagr. 13. The seasonal changes in the abundance of big insect larvae in Lakes Blåsjön and Ankarvattnet.

and an increase during July and the months October and November (Diagr. 13).

In both lakes the first hatching is that of the *Plecoptera* which leave the bottoms in early spring prior to the breaking-up of the ice. Starting from the beginning of June hatching *Plecoptera*, *Ephemeroptera*, and *Trichoptera* are then found throughout the summer in the surface layers of Ankarvattnet. The greatest number of species occurs in June for *Plecoptera*, in July for *Ephemeroptera*, and in August for *Trichoptera*. This sequence holds good also for Blåsjön, where, however, the reduction of species has brought about a more marked delimitation of the hatching periods. As far as can be judged from hatching experiments and qualitative samplings at the surface of the water, hatching *Plecoptera* occur exclusively in April—June, *Ephemeroptera* in July only, and *Trichoptera* almost exclusively in August.

Block bottoms

Upon the block bottoms of Ankarvattnet the average density of population of large-sized larvae of insects can be calculated at 78 individuals per sq.m. The examined slabs of schist are found in the depth zone 0—1 metre. An examination of corresponding regions in Blåsjön revealed no larvae of insects.

In spring the fauna is dominated by *Ephemeroptera* and *Plecoptera*. With

few exceptions their larvae seem to occur as late stages, often ready for immediate hatching. With the progress during the summer of the hatching the abundance drops, and a new colonization comparable with that of the soft bottoms could not be observed.

Larvae of *Trichoptera* are missing in spring. In the course of the summer a very intense new colonization takes place that accounts for the high density of individuals starting with the beginning of August (Diagr. 13). Almost without exception the young larvae settle upon the lower side of the slabs of schist. This remark applies, moreover, to all larval stages of *Ephemeroptera* and *Plecoptera*. In the middle of August a spreading of the population of *Trichoptera* takes place also towards the upper side of the slabs. An analysis of the distribution at the end of August reveals a roughly uniform distribution upon upper and lower side. No appreciable reduction of the population seems to have occurred.

Soft sedimentary bottoms

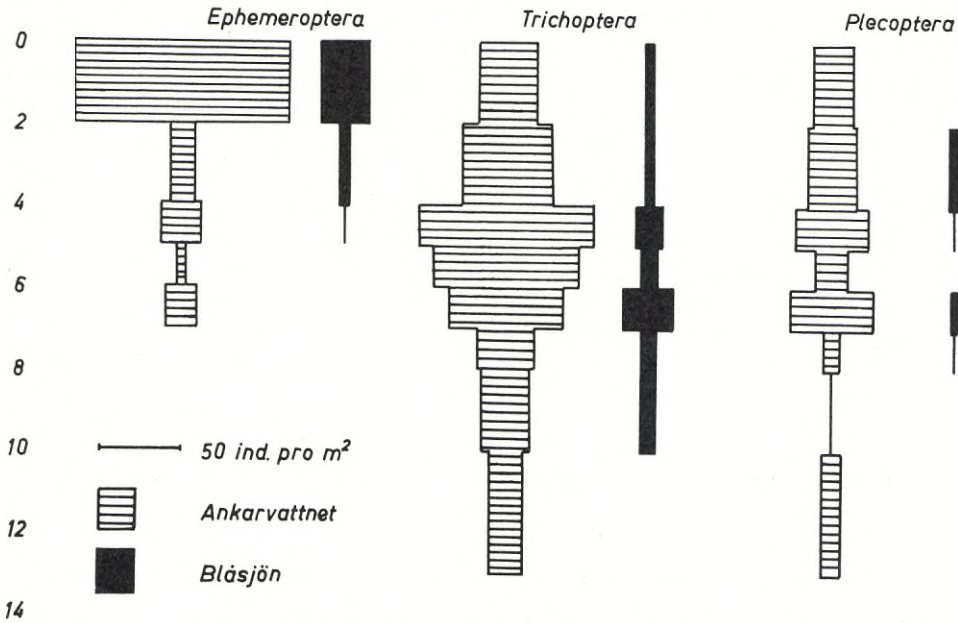
The abundance of big larvae of insects in the soft bottoms of the littoral of Ankarvattnet amounts to 119 individuals per sq.m. For all the littoral regions in Blåsjön the corresponding figure is 16 individuals per sq.m. If only those regions are taken into account which are not influenced by inflows, and which are thus most closely comparable to the examined sections in Ankarvattnet, the comparable figure for Blåsjön becomes 10 individuals per sq.m. Thus the losses can there be estimated at more than 90 per cent.

The bathymetric distribution of the larvae can be seen in Diagr. 14. In Ankarvattnet the *Ephemeroptera* occupy the upper littoral only with a distinct preference of its uppermost two metres. *Trichoptera* as well as *Plecoptera* exhibit wider bathymetrical limits, and are distributed over the entire littoral with a tendency towards greatest abundance in its middle part.

In the regulated Blåsjön the essential depth zoning is retained. Thus the *Ephemeroptera* exhibit a greatest abundance in the upper, and *Trichoptera* and *Plecoptera* in the middle littoral. There exists, however, a development towards total reduction of the different groups of insects with regard to their bathymetric distribution in the more peripheric regions. This tendency towards stenobathic distribution in Blåsjön has been established above also for *Chironomidae* and *Empididae*.

The wealth of individuals of *Ephemeroptera* as well as of *Trichoptera* is greatest in the regions of inflow. The scarce *Plecoptera* seem to be uniformly distributed.

Within the depth region that is populated by larvae of *Ephemeroptera*, i.e. the zone 0—6 m., the density of individuals is 18 individuals per sq.m. in bottoms under the influence of inflow, and 1 individual per sq.m. only in the rest. The corresponding figures for *Trichoptera* are valid for the entire littoral, and amount to 16 and 7 individuals per sq. m., respectively. For *Plecoptera* the figures are 2 and 1 individuals per sq.m.



Diagr. 14. The bathymetrical distribution of big insect larvae in Lakes Blåsjön and Ankarvattnet.

Some remarks about the reaction of individual species to the regulation

Ephemeroptera

Of the *Ephemeroptera* which appertain mainly to the block bottoms of Ankarvattnet, viz. *Ameletus inopinatus* Eat. and *Heptagenia fuscogrisea* Retz., only the former is encountered in Blåsjön after the regulation. The species is missing in the quantitative material, but occurs in very small numbers of hatching individuals in the surface water. As far as can be judged from the few individuals even in the qualitative material, the occurrence in Blåsjön can be considered as very sparse.

In the soft bottoms of Ankarvattnet *Centroptilum luteolum* Müll. is the dominating ephemerid. Among others can be mentioned: *Leptophlebia vespertina* L., *Siphonurus lacustris* Eat., *Paraleptophlebia cincta* Retz., *Chitonophora krieghoffi* Ulm., and *Ephemerella notata* Eat. With the exception of some isolated finds of *Centroptilum luteolum* the bottoms of Blåsjön now contain only *Siphonurus lacustris*. To it has to be added a species of *Baetis* in the regions of the inflows. This has been brought in with the running water.

Siphonurus lacustris does not seem to be limited exclusively to bottoms in front of larger feeders, but appears scantily all around the lake, preferably in connection with small feeders. Without detailed autecological investigations

it is difficult to point to the reason for this occurrence. BENGTSSON (1913) notes that the eggs of *Siphonurus* are characterized by a very thick chorion with fibrillar structure. It could be imagined that the thick envelope of the eggs provides a protection from low temperatures, and that on this account the species survives the freezing-in in the bottoms.

Plecoptera

12 species have been reported from Blåsjön before the regulation (BRINCK 1949). The greater part of the material is derived from the samples collected by MÄÄR. Some of the species belong to the running water. The material from Ankarvattnet contains 8 species.

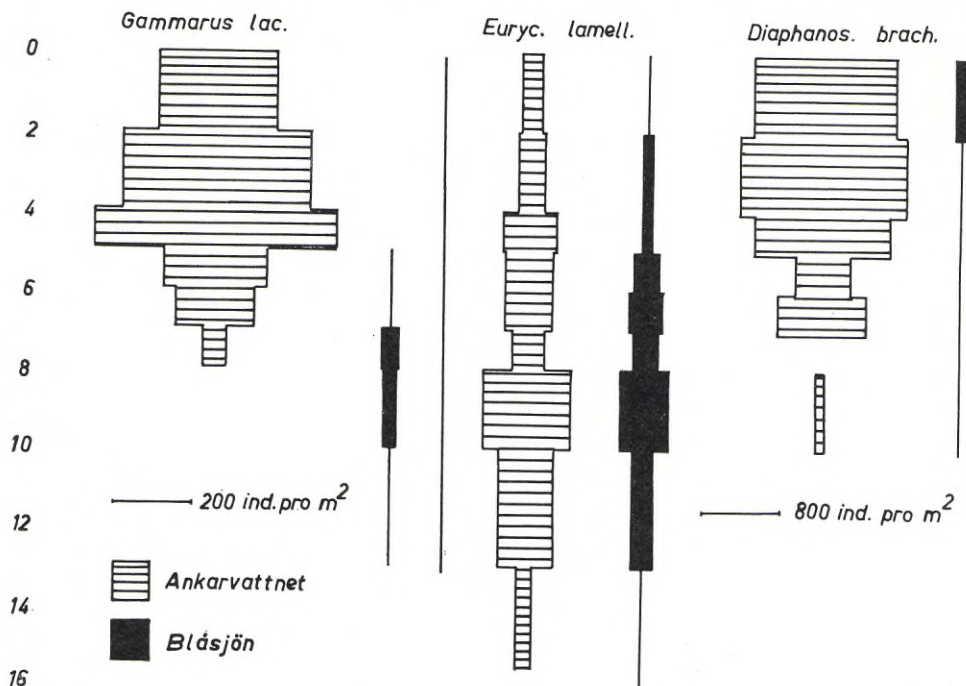
In the regulated Blåsjön only *Diura bicaudata* L., *Capnia atra* Mort., *Nemoura avicularis* Mort., and *Nemoura cinerea* Retz. are left. The plecopterous fauna of Ankarvattnet is dominated by the three first-mentioned species in combination with *Nemoura strandfussi* Ris. occurring on the block coasts. This is in agreement with the statement by BRINCK (1949) who considers these species as eucoenotic for high mountain lakes. The eurytopic *Nemoura cinerea* is sparsely represented in both lakes.

Of the larvae populating Blåsjön in autumn probably only those which are found below the draw down limit hibernate and hatch in the following year. These more deeply situated littoral zones are likewise the source for the hatching of *Capnia atra* in April—June and of *Nemoura avicularis* in June. *Diura bicaudata*, which is found along the water's edge in June, seems to invade the regulated area, and to pass it during its hatching *pari passu* with the rise of the water.

Trichoptera

15 species have been observed in the unregulated Blåsjön and in Ankarvattnet. Among the genera represented by a greater number of individuals can be mentioned *Apatania* and *Apatidea*, characteristic amongst others for the Swedish high mountain lakes (FORSSLUND 1931), and *Agrypnia* and *Polycentropus*.

Of the two species of *Apatania*, viz. *A. stigmatella* Zett. and *A. wallengreni* Mc Lachl., from our area the regulated Blåsjön contains *A. stigmatella* only. This species occurs in all depth zones of the littoral, and can be considered as the most common species of *Trichoptera* in Blåsjön in its regulated condition. In addition to this species there occur, more restricted to bottoms below the draw down limit, *Agrypnia obsoleta* Hag., *Mystacides azurea* L., and *Polycentropus flavomaculatus* Pict. which can be considered as eurytopic. Finally there remains in Blåsjön the arctic to high boreal species *Agraylea cognatella* Mc Lachl. which after the regulation is found most frequently in connection with the narrow and thinly growing belt of *Nitella* which runs around the lake immediately below the drawdown limit, and is better defined in the regions that are influenced by inflowing water.



Diagr. 15. The bathymetrical distribution of some Crustacea in Lakes Blåsjön and Ankarvattnet.

Coleoptera

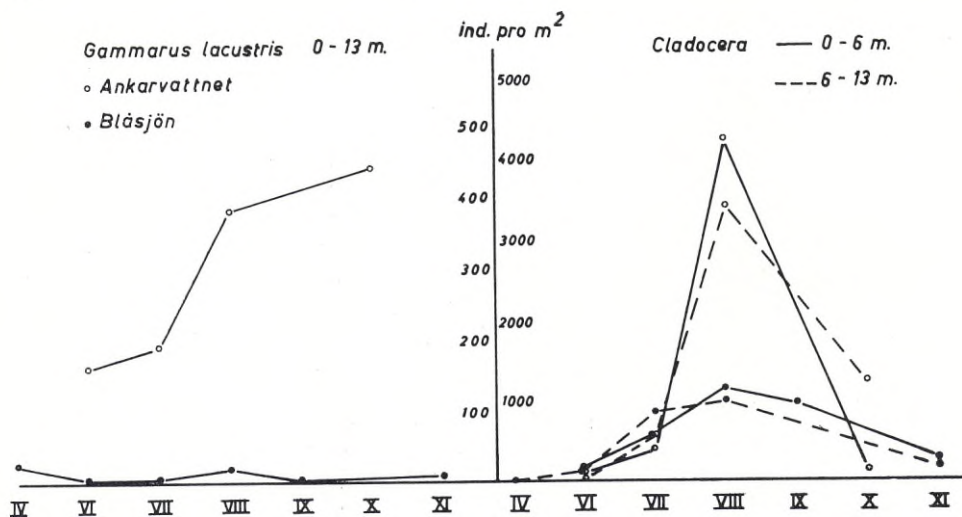
The coleopterous fauna is dominated in either lake by hydropterines. Their larvae and imagines occur roughly uniformly distributed down to 10 m in Ankarvattnet and to a depth of 7 m in Blåsjön, the density being 9 and less than 1 individual per sq.m., respectively. *Deronectes griseostriatus* Deg. is the dominating species in either lake. Especially in Ankarvattnet there occur likewise *Haliplus fulvus* Fabr. and representatives of the genera *Ilybius* and *Hydroporus*.

Crustacea

Amphipoda, Isopoda

Both *Grammarus lacustris* Sars and *Asellus aquaticus* L. have been reported from Blåsjön prior to the regulation. Of these *Asellus* seems to have been feebly represented in the lake, while the more abundant *Gammarus* appears in the uppermost 8 metres of the littoral, with a greatest abundance between 2 and 6 metres. The vertical distribution of *Gammarus* in Ankarvattnet can be seen in the Diagram 15 which shows agreement with the distribution in Blåsjön before the regulation.

In the regulated Blåsjön *Asellus aquaticus* is altogether missing, and the number of individuals of *Gammarus lacustris* has dropped considerably



Diagr. 16. The seasonal changes in the abundance of some Crustacea in Lakes Blåsjön and Ankarvattnet.

(cf. NILSSON 1961). A similar decrease in connection with regulation is known e.g. from other lakes (DAHL 1926, 1932, HUITFELDT-KAAS 1935, STUBE 1958, AASS, private communication).

The Diagram 15 shows that in Blåsjön *Gammarus* occurs almost exclusively below the draw down limit. Within the zone 5—6 m 1 specimen only has been encountered. *Gammarus* seems to be bound mainly to areas with a fairly good supply of fresh organogenic detritus or vegetation, i.e. to major accumulations of detritus in the inflow regions or to the growths of *Nitella*. By comparison with the supplies in Ankarvattnet the probable losses in the regulated zone of Blåsjön can be calculated at 100 per cent, and in the remaining littoral regions at over 80 per cent. As the result of the increasing density of individuals in Ankarvattnet in the course of the summer the differences between the lakes are accentuated towards the autumn (Diagr. 16).

Cladocera

The majority of species of *Cladocera* which have been encountered in Ankarvattnet and Blåsjön exhibit affinities to bottoms or zones near the bottom. For many crustaceans which are generally labelled as planktonic organisms this tendency has been established in other lakes by transverse sections through the open water.

Of the 18 species occurring in the bottom samples from Ankarvattnet and Blåsjön a few only exhibit a preponderately planktonic trend. To these can be counted first of all *Bosmina coregoni* Baird and *Daphnia longispina* Müll. (cfr. LÖFFLER 1952). Among other cladocerans which occasionally

Table 10. The percentages of different species of *Cladocera* in bottom samples from Lakes Blåsjön and Ankarvattnet.

	Blåsjön	Ankarvattnet
<i>Eurycercus lamellatus</i> MÜLL.	37 %	30 %
<i>Holopedium gibberum</i> ZADD.	11	1
<i>Iliocryptus acutifrons</i> SARS.	10	3
<i>Ophryoxus gracilis</i> SARS.	9	1
<i>Bosmina coregoni</i> BAIRD.	9	3
<i>Alona quadrangularis</i> MÜLL.	7	< 1
<i>Simocephalus vetulus</i> MÜLL.	6	3
<i>Acroperus harpae</i> BAIRD.	3	—
<i>Diaphanosoma brachyurum</i> LIEV.	2	55
<i>Ceriodaphnia pulchella</i> SARS.	2	1
<i>Daphnia longisina</i> MÜLL.	1	2
<i>Camptocercus</i> sp.	1	—
<i>Polyphemus pediculus</i> L.	< 1	< 1
<i>Bythotrephes longimanus</i> LEYD.	< 1	—
<i>Chydorus sphaericus</i> MÜLL.	< 1	—
<i>Lathonura rectirostris</i> MÜLL.	< 1	< 1
<i>Macothrix</i> sp.	< 1	—
<i>Alonopsis elongata</i> SARS.	< 1	—

appear in plankton samples can be mentioned: *Holopedium gibberum* Zadd., *Polyphemus pediculus* L., and *Bythotrephes longimanus* Leyd. The occurrence of the species in the bottom samples can be explained to a large extent by a sedimentation from the open water. Worthy of notice are, however, the wealth of individuals in the bottom sediments and the vertical zoning of the individual species, the greatest numbers of individuals occurring at different depths. *Holopedium gibberum* thus occurs in Blåsjön at all depths, but with a well marked maximum of individuals between 8 and 10 metres. *Bosmina coregoni* occurs from 0 to 30 metres, and shows a distinct maximum of individuals in the topmost two metres (GRIMÅS 1959).

To the species with a greater wealth of individuals that are bound mainly to bottoms or to zones near the bottom can be counted: *Eurycercus lamellatus* Müll., *Diaphanosoma brachyurum* Liev., *Iliocryptus acutifrons* Sars, *Ophryoxus gracilis* Sars, *Alona quadrangularis* Müll., *Simocephalus vetulus* Müll., and *Acroperus harpae* Baird.

One of the more important changes in the *Cladocera* after the regulation is the decrease of *Diaphanosoma brachyurum*. *Eurycercus lamellatus*, which together with *Diaphanosoma* dominates the cladoceran fauna of Ankarvattnet (see Table 10), suffers no influence in this direction. The explanation probably lies in the vertical distribution of the species which is not altered by the regulation. In Ankarvattnet as well as in Blåsjön *Eurycercus* is orientated towards the middle and lower littoral (Diagr. 15) (cf. EKMAN 1915). For this reason the population is only in part directly influenced by the regulation, in contrast to *Diaphanosoma* which in either lake inhabits the upper portions of the littoral (Diagr. 15).

For the planktonic forms in Blåsjön before the regulation (LÖFFLER 1952) as well as for the *Cladocera* in Ankarvattnet and in Blåsjön after the regulation the greatest abundance falls in August (see Diagr. 16). The great differences in the quantity of benthonic *Cladocera* appertain to this month, depending, amongst others, upon the elimination of *Diaphanosoma brachyurum* from the regulated lake. During autumn the density of individuals decreases gradually in order to reach minimum and identical values in both the unregulated and the regulated lake. These conditions last from the beginning of November to the end of June in the following year. Some observations indicate, however, that in the regulated lake the production of *Cladocera* is intensified at a somewhat earlier date. As an example we can mention that according to LÖFFLER *Holopedium gibberum* in Blåsjön attains the greatest number of individuals in September. According to plankton samples as well as bottom samples this maximum was reached in the regulated Blåsjön, in 1956 as well as in 1957, already in July.

It is established that a regulation results in an intensified production of *Cladocera*. This has been proved by direct examinations of the bottom fauna (DAHL 1926, 1932, HUITFELDT-KAAS 1935, RUNNSTRÖM 1946, 1955, AASS, private communication, GRIMÅS 1959, GRIMÅS and NILSSON 1961), but has been established also indirectly by an altered choice of food especially of the char (e.g. RUNNSTRÖM 1951, NILSSON 1955, 1961). The increased abundance has been connected mainly with the drowning of further areas of the shore. The phenomenon has also proved to be of a passing nature. A similar effect will probably be the result of every interference with a lake that implies a redeposition of sediment, e.g. an increased lowering of the surface.

On the basis of, amongst others, detailed examinations of the food habits of the fish in Blåsjön before and after the regulation (NILSSON 1955) a similar flourishing can be established in Blåsjön. This ought to apply first of all to 1949 and some of the following years. The examinations of the bottom in 1956 and 1957 show, however, that this positive effect has been subject to a gradual waning that can be connected with the progressive leaching-out of the regulated region. The average density of the population of *Cladocera* is 1,359 individuals per sq.m in the bottoms of Ankarvattnet and 438 in those of Blåsjön, indicative of a deficiency in Blåsjön of more than 65 per cent.

For *Eurycercus lamellatus*, which on account of its size, wealth of individuals, and availability forms an important animal of prey for the fish, it has been found both in Blåsjön and in other regulated waters that it not only increases in abundance immediately after the regulation, but also retains its dominating position in the cladoceran fauna. The results in Blåsjön in 1956—1957 show also that this species becomes scarcer after a number of years. In Ankarvattnet as well as in Blåsjön the species occurs down to a depth of 30 m, and the deficiency in Blåsjön can be calculated at 50 per cent in this

zone as well as in the littoral. The species is most numerous in August in either lake, but can be observed in samples taken as late as October—November.

Other Crustacea

In both lakes the *Copepoda* have their minimum abundance in June, and are most numerous in August—September. Quantitatively the *Cyclopidae* dominate, *Cyclops scutifer* Sars being numerous during the summer months. While the water is covered with ice *Macrocyclus albidus* Jurine and *Megacyclus viridis* Jurine occur together in the bottom sediments. Species of *Diaptomus* appear in bottom samples after the beginning of July. *Hetercope saliens* Lilljeb. is not found before autumn (September—October).

The average density of individuals in the bottoms of Ankarvattnet can be calculated at 2,030 per sq.m. For Blåsjön this figure is 991.

Representatives of the *Ostracoda* are found in small numbers both in Ankarvattnet and in Blåsjön (13 and 15 individuals per sq.m, respectively). The maximum abundance in Blåsjön falls into spring, while the lake is still covered with ice.

Hydracarina

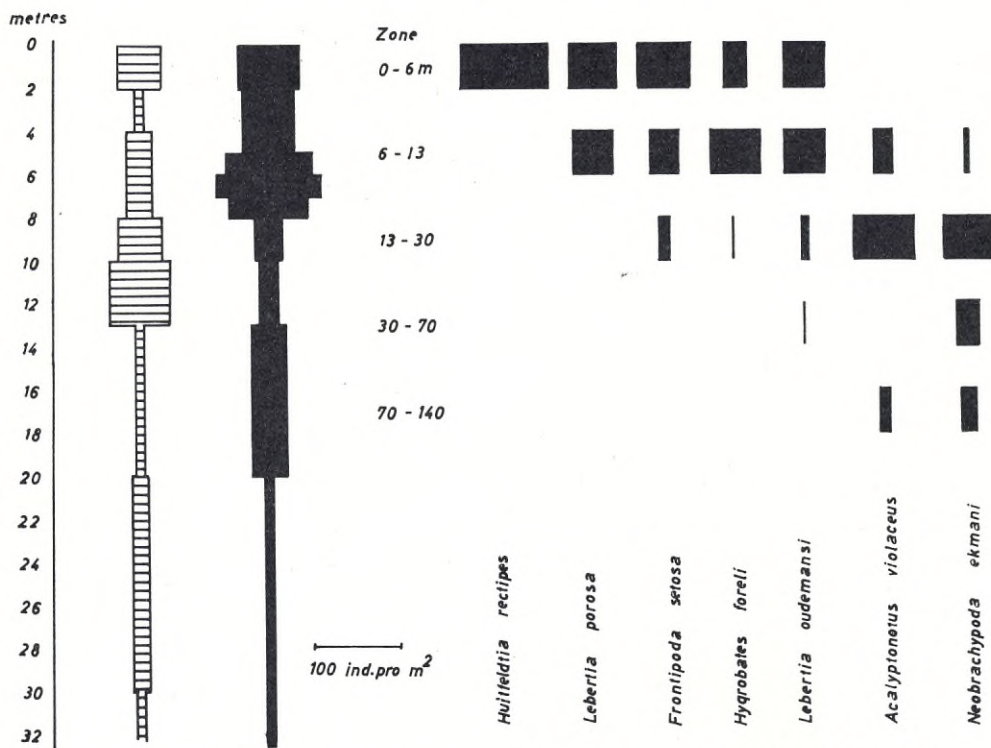
Thanks to a detailed study by Prof O. LUNDBLAD of the Riksmuseum, Stockholm, of the material of *Hydracarina* the distribution of the species in Blåsjön after the regulation can be given (Tab. 11).

From the quantitative point of view we can first of all establish that the wealth of individuals in the bottoms of Blåsjön is about twice as great as in those of Ankarvattnet, viz. 59 and 32 individuals per sq.m, respectively. The greater abundance in Blåsjön can probably be explained by the general

Table 11. The percentages of the different species of *Hydracarina* in the regulated Lake Blåsjön.

<i>Frontipoda setosa</i> KOEN.	26 %
<i>Lebertia porosa</i> THOR.	22
<i>Lebertia oudemansi</i> KOEN.	16
<i>Huitfeldtia rectipes</i> THOR.	14
<i>Acalyptonotus violaceus</i> WALT.	6
<i>Neobrachypoda ekmani</i> WALT.	5
<i>Hygrobates foreli</i> LEB.	4
<i>Arrenurus stjördalensis</i> THOR.	2
<i>Sperchon squamosus</i> KRAM.	1
<i>Pionacerus leuckarti</i> PIERS.	1
<i>Hydrochoreutes ungulatus</i> KOCH.	1
<i>Piona pusilla</i> f. <i>rotundoides</i> THOR.	< 1
<i>Tiphys lapponicus</i> NEUM.	< 1
<i>Piona pusilla</i> NEUM. s.str.	< 1
<i>Neumania callosa</i> KOEN.	< 1
<i>Atractides nodipalpis</i> THOR.	< 1
<i>Arrenurus membranator</i> THOR.	< 1

Number of species 17, number of individuals 636.

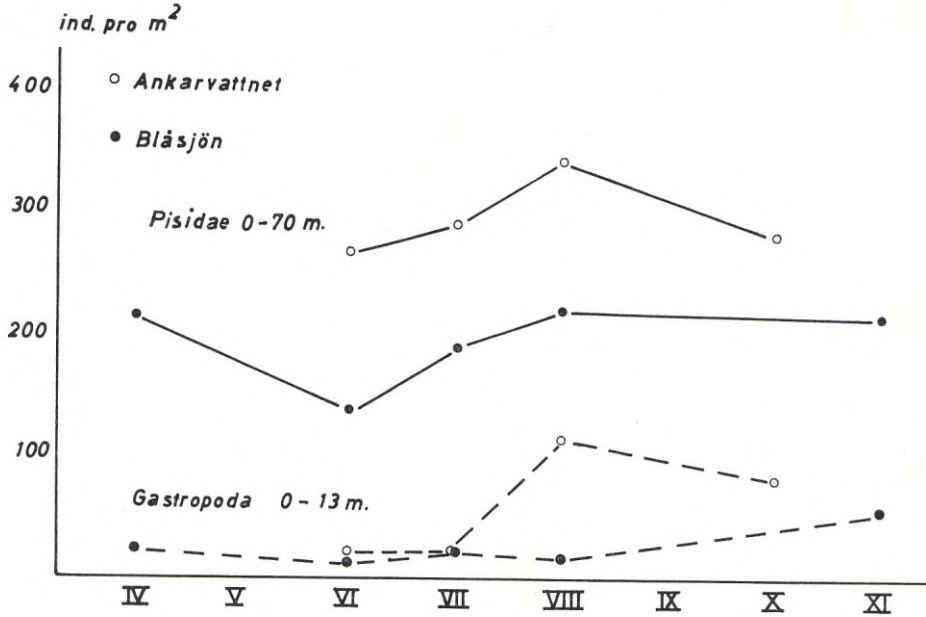


Diagr. 17. Bathymetrical distribution of Hydracarina in Lake Blåsjön (black) and Lake Ankarvattnet (parallel lines).

resistance of the animals to drying-up (LUNDBLAD 1930) and by the access to suitable food also within the regulated area (cf. p. 226).

The *Hydracarina* occur in both lakes down to the greatest depths, but the majority of the species is limited to the littoral. The orientation towards the deeper portions of the littoral which can be observed in Ankarvattnet occurs also in Blåsjön in the neighbourhood of the draw down limit (Diagr. 17). The diagram shows likewise the relative distribution of the most important species in the different depth zones.

Descriptions (LUNDBLAD 1927) from natural, i.e. unregulated, waters within the region agree in bathymetric respect on the whole with the conditions in the regulated Blåsjön. For the unregulated Blåsjön *Lebertia* ssp. has been reported from the depth interval 2—20 m, with the greatest abundance in the upper littoral, and *Acalyptonetus violaceus* and *Piona pusilla* f. *rotundoides* from the middle littoral. For Ankarvattnet can be mentioned *Lebertia porosa* and *Piona pusilla* f. *rotundoides* from the upper littoral, *Frontipoda setosa* from the lower littoral, and *Neobrachypoda ekmani* from the regions of the profundal.



Diagr. 18. Seasonal changes in the abundance of Mollusca in Lakes Blåsjön and Ankarvattnet.

Mollusca

Pisidae

In the course of the studied months the abundance of the *Pisidae* that are characteristic for the type of lake is not subject to any major changes in either of the lakes. In Ankarvattnet the density of individuals varies between 268 and 344 individuals per sq.m. For Blåsjön the corresponding figures are 137 and 220. In both lakes the minimum abundance falls into June, the maximum into August (Diagr. 18). The average density of individuals is 298 individuals per sq.m in Ankarvattnet and 185 in Blåsjön, indicating a deficiency of 38 per cent for Blåsjön.

Pisidae occur in Ankarvattnet at any depth, the greatest abundance being found in the regions of the profundal (Diagr. 11). The decrease in abundance observed in other lakes in the middle littoral (LUNDBECK 1936, BRUNDIN 1949) applies likewise to Ankarvattnet.

The specific composition of the fauna and its bathymetric distribution is characteristic for northern oligotrophic lakes (cf. VALLE 1927, BRUNDIN 1942). The dominant species *Pisidium conventus* Cless occurs within very wide bathymetric limits, and has been found in Ankarvattnet and the unregulated Blåsjön from the uppermost littoral down to the greatest depths. A similar vertical distribution can be established for *P. cinereum* Ald. Of great qualitative importance is *P. lilljeborgi* Cless. which is, however, restricted to the

Table 12. The vertical distribution of *Pisidae* in the littoral of Lake Blåsjön after regulation.

Depth zone	Ind. per sq. m.
0—2 metres	—
2—4	—
4—5	47
5—6	204
	draw down limit
6—7	311
7—8	293
8—10	216
10—13	298

littoral. The littoral contains furthermore, but more sparsely, *P. obtusale* Pfeiff., *P. nitidum* Jen., and *P. subtruncatum* Malm.

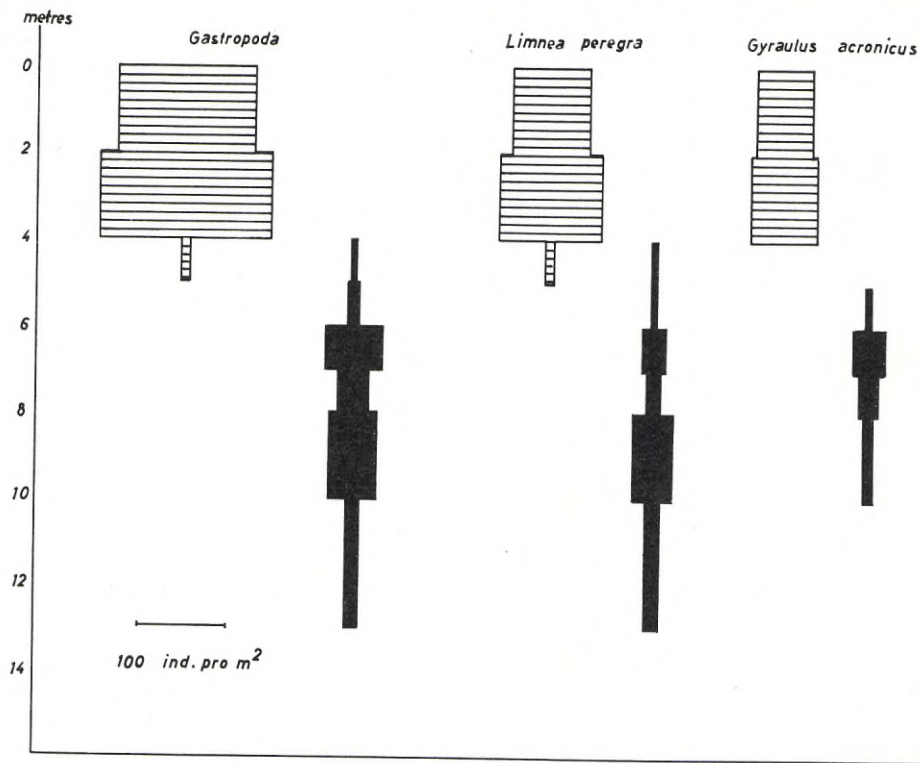
After the regulation the *Pisidae* are altogether lacking in the depth interval 0—4 metres. The decrease of abundance in the middle littoral which is characteristic for unregulated lakes is not found in the regulated Blåsjön (Diagr. 11). We rather find in the depth zone 6—8 m one of the regions richest in individuals and an abundance that is greater than in Ankarvattnet. Also the greater abundance immediately above the draw down limit in the depth zone 4—5 m is worthy of notice (Tab. 12). This distinct limit at the depth of 5 m has been observed above, e.g. in the specific distribution of the *Chironomidae*, and is discussed more fully in Chapt. 5. The dense vegetation of *Nitella*, which is disadvantageous for filtering organisms, is reduced by the regulation, and this had led to an amelioration of the conditions for *Pisidae* within this limited region.

Within the bare sedimentary bottoms following below the depth of 8 m losses become again noticeable. A similar reduction within the profundal has been established also in American storage lakes (CUERRIER 1954, RAWSON 1958). The causes of this reduction are discussed in Chapt. 5 (cf. GRIMÅS and NILSSON 1961).

Gastropoda

As for many other groups of animals the differences in the density of individuals between Ankarvattnet and Blåsjön are accentuated also for the *Gastropoda* in the month of August, when the abundance in Ankarvattnet rises considerably (Diagr. 18). In the littoral the average density of individuals is 53 per sq.m in Ankarvattnet, and 23 in Blåsjön. Thus the deficiency in Blåsjön can be estimated at 57 per cent.

The bathymetric distribution in the two lakes exhibits very essential differences. In Ankarvattnet the gastropods are entirely limited to the upper half of the littoral, viz. 0—5 m (Diagr. 19). In Blåsjön they are altogether absent from the zone 0—4 m, and occur instead depressed to the lower half



Diagr. 19. Bathymetrical distribution of Gastropoda in Lake Blåsjön (black) and Lake Ankarvattnet (parallel lines).

of the littoral, viz. 4—13 m. Thus the regulation has brought about a widened bathymetric amplitude. The losses in the regulated zone of Blåsjön which can be estimated at 96 per cent are thus counterbalanced to a certain extent by the occurrence below the draw down limit.

In Ankarvattnet as well as in Blåsjön both before and after the regulation we find two species, viz. the eurytopic *Limnea peregra* Müll. and *Gyraulus acronicus* Fer., a species, with a northern distribution (HUBENDICK 1947). *Limnea peregra* which in both lakes occurs in two forms, viz. *ovata* and *peregra*, accounts in Ankarvattnet for 61 per cent and in Blåsjön for 60 per cent of the gastropod fauna. There is thus no reason to assume a change in the balance between the two species as the result of the regulation. In both lakes *L. peregra* exhibits the greatest bathymetric amplitude, with an orientation towards a somewhat greater depth than *Gyraulus acronicus* in Blåsjön (Diagr. 19).

Oligochaeta

The oligochaetes occur in both lakes within all depth zones, and form, after the *Chironomidae* and the *Cladocera*, the group of animals richest in individuals in the bottom fauna. Representatives of the family *Naididae* are dominant. Both lakes contain in addition *Lumbriculidae* and *Chaetogastridae*.

For the whole of Ankarvattnet the density of individuals is 718 individuals per sq.m. For Blåsjön it is 405. The maximum abundance falls into July and August. The greatest losses are found in the regulated zone, where the deficiency in Blåsjön can be calculated to 84 per cent (Ankarvattnet 901, Blåsjön 146 individuals per sq.m). This deficiency is partly counterbalanced in Blåsjön by a greater abundance in other parts of the littoral (Ankarvattnet 500, Blåsjön 750 individuals per sq.m.) (Diagr. 11).

To the whole of the littoral applies the observation that the abundance is greater in the regions of inflow, being about twice as great in the regulated area. The general tendency towards a greater density of individuals in the eastern parts of St. Blåsjön and L. Blåsjön especially with regard to *Lumbriculidae* can be explained as the result of a higher content of organogenic detritus in these regions (see discussion, p. 189, and Diagram 4).

Remaining groups of the bottom fauna

Hirudinea occur in both lakes in small numbers. The material includes only one species, *Glossosiphonia complanata* L., which in Ankarvattnet occupies the upper littoral and in Blåsjön is found within the depth zone 5 to 8 metres.

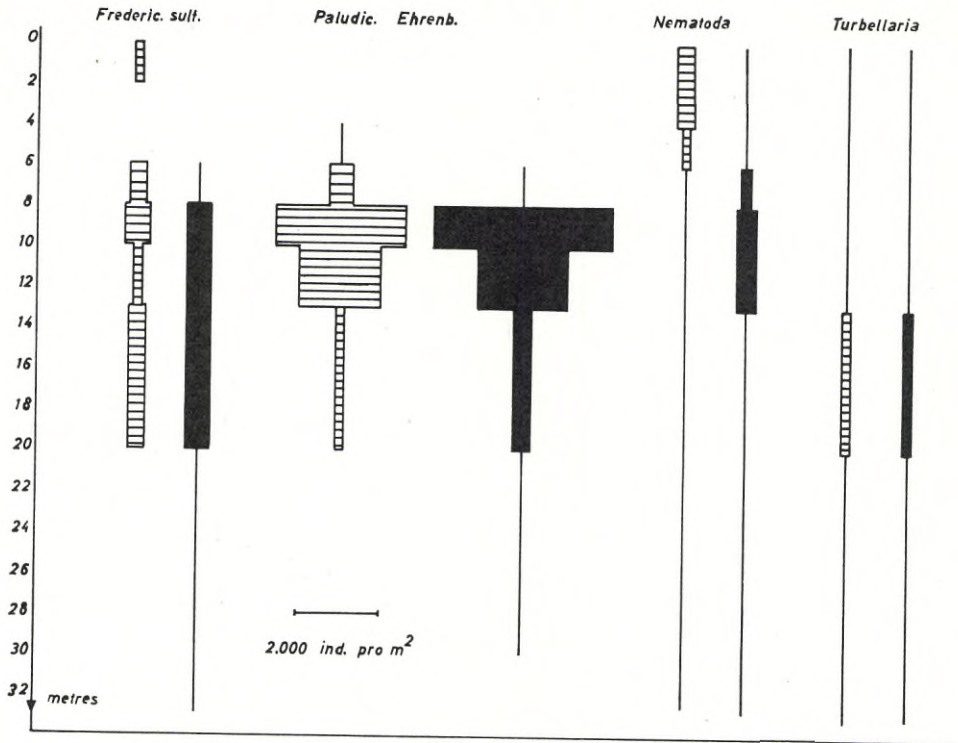
The maximum abundance of the *Nematoda* is situated in the upper littoral of Ankarvattnet (437 ind. pro m² in the zone 0—2 metres). In Blåsjön this maximum occurs below the draw down limit (423 ind. pro m² in the zone 8—10 metres) (Diagr. 20). The relative share of the entire fauna has to a small degree increased after the regulation.

Like the nematods the *Turbellaria* appear in all depth zones of the lakes with maximum abundance in the upper profundal in both lakes (Diagr. 20).

Hydrozoa are present in the bottoms of Ankarvattnet during the whole summer, but are most abundant in autumn on the larger plants, in the block zone, etc. They belong almost exclusively to the upper littoral, but are found in small numbers down to 17 metres depth. In Blåsjön the *Hydrozoa* occur between 2 and 30 metres depth, sparsely in the regulated area and with a maximal abundance immediately below the draw down limit (Diagr. 11).

Bryozoa are for different reasons not included in the discussion of the entire fauna. In both lakes they occur mainly in the middle and lower parts of the littoral.

The balance between the two species in the material has not changed after the regulation. *Paludicella Ehrenbergii* van Ben. covers 74.9 per cent of the



Diagr. 20. Bathymetrical distribution of some bottom animals in Lake Blåsjön (black) and Lake Ankarvattnet (parallel lines).

Bryozoa in Blåsjön and 75.0 per cent in Ankarvattnet. The remaining percentage belongs to *Fredericella sultana* Blumenb.

Except for losses in the regulated area the bathymetrical distribution corresponds with that in Ankarvattnet (Diagr. 20) with a tendency towards higher abundance in Blåsjön.

5. General changes in the benthic environment and their effect upon the fauna

The temperature factor

In the above, changes with increasing altitude of lakes have been established in the natural balance between the main groups of the Chironomidae, and even the effect of the regulation on this balance. It could likewise be shown that by regulation the bathymetric distribution of the main groups within the lake becomes more accentuated.

Changes in the temperature conditions can be considered to constitute an important explanatory factor. The climatological conditions during early

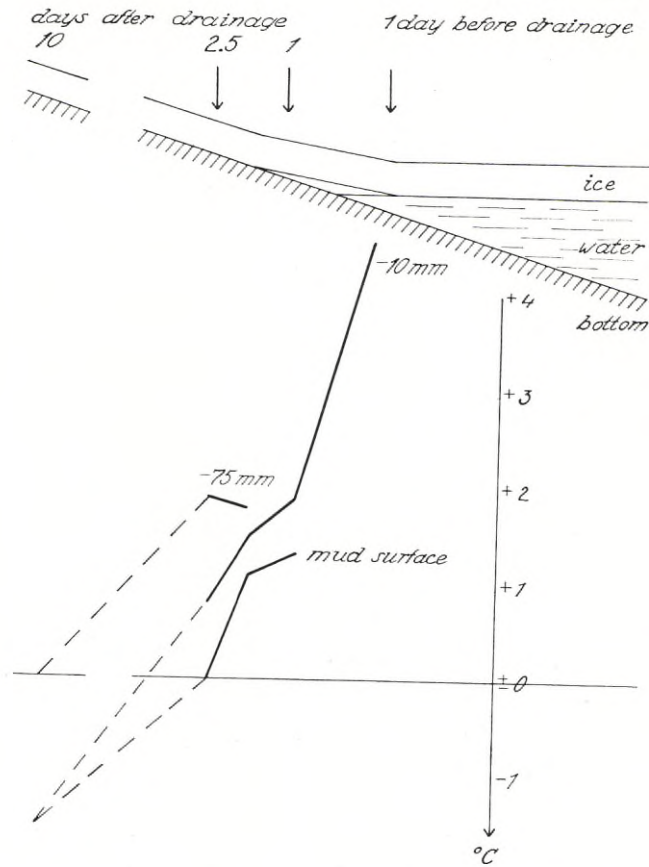
winter seem to be of great importance. As an example we can mention the dominating position of the *Orthocladiinae* in the lake Torneträsk (THIENEMANN 1941). In this case special consideration should be paid to the late covering of the lake with ice and the low temperature of the entire mass of water, e.g. 0.61°C at the depth of 60 m on April 17, 1949 (EKMAN 1957).

The comparison between the different depth regions can be carried out upon the same basis. In Ankarvattnet the upper littoral seems to obtain its character mainly through the low temperature of the water during the winter half of the year. The importance of the winter temperature as a limiting factor for the composition of the biocoenosis is underlined by the observation that the trophic standard in the active surface layer of the soft bottoms seems to be homogeneous in the entire littoral. Within the studied areas the upper littoral exhibits organogenic sediments with a desirable loose contact layer in the surface zone against the water. The submerged vegetation mitigates the eroding effect of the waves even on an unstable surface layer and preserves the organogenic sediments by means of the binding power of its root system. The same conditions for the upper littoral have been established in other unregulated sub-arctic lakes, e.g. in Kultsjön in southern Lapland.

The regulation renders the climate more severe. Of decisive importance for the temperature conditions in the bottoms is the situation in winter, when the surface of the water is near the draw down limit. The bottoms of the regulated zone are exposed to freezing, and during the same time the fauna below the draw down limit lives under conditions that characterize the stagnation of the upper littoral in winter. These areas are, however, out of reach for the fast natural warming-up of the upper water masses in the spring, when the surface of the water coincides again with the damming limit. It can be supposed that this cooling of the bottoms after some time selectively eliminates species with higher demand on warmth or species which during some phase of their development are sensitive to abnormally low temperatures. Low temperatures of this extension, reaching down to the upper profundal, can explain the hegemony of the *Orthocladiinae* and *Tanytarsini* in the regulated Blåsjön, the almost total elimination of the *Chironomini*, the reduction in the entire littoral of chironomids hatching in the spring and the general tendency towards retarded hatching throughout the summer in comparison with the situation in Ankarvattnet. It must, however, be emphasized that this selection need not take place with immediate effect, but can be conceived as a slow process (cf. NILSSON 1961).

Temperature observations in bottoms affected by drainage

In order to arrive at an opinion about the temperature conditions in bottoms during the lowering of the water-level a reconnoitering investigation has been carried out in Lake Ransaren in southern Lapland in January 1958.



Diagr. 21. Temperature conditions in bottoms of Lake Ransaren, affected by drainage.

The measurements were taken with thermistors, Western Electric 14 B. At the time of the investigation the surface of the water was being lowered 12 cm a day, the temperature of the air being -17.0°C .

Where the ice rests upon dried-up bottoms, a sheet of ice, about 10 mm thick, is intercalated. This sheet is frozen to the ice, but easily split off in the region close to the sinking surface of the water. Upon the bare sedimentary bottoms the uppermost layer of the sediment is frozen into this sheet. This phenomenon has been established also in Kultsjön after the first lowering of the water-level in the winter, 1959.

This thin sheet of ice between the bottom and the ice is probably formed when ice comes in contact with the sediment. From the following it will be seen that at the time of this contact the sediment contains a considerable amount of heat. The heat, liberated from the sediment is able to melt the lower surface layer of the ice, and the water thus produced forms the ice sheet together with the water retained in the bottom. After the exhaustion of the stored-up heat the ice sheet freezes more intimately to the ice, and the freezing continues down into the sediments.

The results are represented in Diagram 21. The high temperatures in the sediment immediately before the drainage are remarkable. Thus at a depth of 10 mm below the surface of the mud $+4.5^{\circ}\text{C}$ has been measured in a region that was to be dry within 24 hours. The high temperature of the sediment is attributable to the fast lowering of the water surface. This implies at the same time for the fauna a short period with low temperatures prior to the complete drainage. If the bottom animals can be assumed to migrate towards greater depths, such a migration ought not to be initiated by temperatures of the sediment around $+4^{\circ}\text{C}$ which ought to be a normal sediment temperature below the winter littoral. The conditions are accentuated by the great horizontal distance passed by the water's edge in the course of the drainage of regulated lakes.

The capacity of the ice for the freezing in of sediment naturally depends upon the season. In Blåsjön the contact between ice and bottom is of short duration in the zone of one metre's thickness above the draw down limit, and falls in a season, when the thickness of the ice does not grow downwards, i.e. does not freeze in bottoms, in this case. There is, therefore, no reason to expect the formation of an ice-sheet and the rising movement of the ice during the spring flood does not affect the sediment to any great extent. The depth zone 5—6 metres exhibits, in fact, a continuous layer of fine sediments. The observed occupation of the zone by chironomids and the sharply defined limit at the depth of 5 metres even for other bottom animals, e.g. *Pisidae*, can be explained by a combined effect of the supply of fine sediments and the tolerable temperature conditions.

Observations on the reaction of the fauna to low temperatures

In the month of April, after the first lowering of the water-level in 1959, reconnoitering investigations were carried out in Lake Kultsjön, southern Lapland, with the intention of studying the fauna in dried-up and ice-covered bottoms in the zone of regulation. The sampling comprised three vertical layers: 1) the ice of the lake with frozen-in aquatic vegetation consisting of *Nitella* sp. and *Ranunculus* sp., 2) the ice sheet, comprising the layer immediately above the bottom and down to 20 mm in the porous surface layer of the sediment, and 3) not frozen, soft bottom material to a depth of about 50 mm below layer (2).

A comparison of the faunas in these well delimited zones reveals a distinct vertical zoning of the main groups that are represented: insect larvae, gastropods, and crustaceans in zone (1), insect larvae, pisidia, hydracarina, and some few oligochaeta in zone (2), and almost exclusively oligochaeta in zone (3). This zoning seems to agree with that normal in the bottoms, and no major changes due to an extreme fall of temperature have taken place.

After the thawing of the samples 80 per cent of the organisms proved to

Table 13. Fauna of frozen-in bottoms in the regulated area of Lake Kultsjön, 1959.

Zone	<i>Chironomidae</i>	<i>Mollusca</i>	<i>Annelida</i>	Remaining components	Ind. per sq. m.
1.	92.3 %	1.5 %	—	6.2 %	1,625
dead %	30	100	—	100	—
alive %	70	—	—	—	—
2.	55.4 %	29.2 %	13.9 %	1.5 %	1,625
dead %	10	5	20	—	—
alive %	90	95	80	100	—
3.	9.5 %	—	90.5 %	—	924
dead %	100	—	5	—	—
alive %	—	—	95	—	—
					4,174
				dead	19.9 %
				alive	80.1 %

be alive (Table 13). Among the dead animals can be noticed *Gastropoda* and larvae of *Ephemeroptera* in zone 1 and *Hirudinea* in the zones 2 and 3. The great percentual survival of *Chironomidae*, *Pisidae*, and *Naididae* is noticeable. Similar observations have been made by RUNNSTRÖM (1946) in the lake Torrön where he noticed a rich occurrence of living *Pisidae* and larvae of *Chironomidae* in the sediment surface after the melting of the ice cover.

The composition of the chironomid fauna is of special interest. The genus which dominates in connection with the vegetation frozen into the ice is *Paratanytarsus*, while the group of *Tanytarsus gregarius* and species of *Procladius* dominate in the frozen-in surface of the sediment. Both zones contain elements of *Orthocladiinae*.

Dealing with the normal dwelling regions of these chironomids THIENEMANN (1954) reports that *Paratanytarsus* is often found in larval tubes on the vegetative parts of plants. The group of *Tanytarsus gregarius* dwells mainly in the surface of the sediment as builders of tubes. The larvae of *Tanypodinae*, in this case *Procladius*, move about freely in and above the muddy surface. The stability of this orientation even after drastic cooling is remarkable.

About the hibernation of the chironomid fauna in frozen bottoms several observations have been published (ROEDEL 1886, MAYENNE 1933, ANDERSEN 1946). In several cases also the reasons of the resistance to cold have been analysed, e.g. the diminution in the content of free water in larvae of *Chironomus* during the cold season (THIENEMANN 1954 after JABLONSKAJA 1935).

The survival of the fauna has, however, to be considered also as a function of the duration of low temperatures. We remind here of the conditions in the zone of regulation in Blåsjön with a brief contact between ice and bottom in the zone of 5—6 metres. If the bottoms are exposed during a longer

time several successive periods of cold occur. In this case the repeated exposure to critically low temperatures seems to reduce the resistance of the fauna. The established increasing losses from the autumnal larval material of chironomids towards shallower regions in the regulated zone of Blåsjön have to be interpreted as results of the above-mentioned effect.

If the four main groups of the chironomid fauna are studied with regard to their resistance to low temperatures, many results speak in favour of a unique position for the *Tanytarsini*.

Under normal conditions the *Tanytarsini* agree with the *Orthoclaadiinae* in their orientation towards the regions of the upper littoral. As we have seen the position of the *Tanytarsini* within the entire littoral becomes more accentuated after regulation and appears equivalent to that of the *Orthoclaadiinae*. It is likewise characteristic that the first chironomids which leave the bottoms of the regulated region during the early summer are representatives of the *Tanytarsini*. The high percentage of survival in the ice and the frozen bottoms of Kultsjön also speak in favour of their resistance to cold.

Conditions of alimentation

As has already been established, the regulation causes a complete elimination of macrophytes within the regulated area. Only some sparse stands of *Nitella* remain under the draw down limit. The importance of the vegetation for a rich animal life is known especially on account of its being a primary producer. The great reduction, which even befalls the sedentary micro-vegetation deprives the fauna of a direct source of food. Consequently, those animals, which are directly dependent upon this supply of fresh vegetation, are parallelly eliminated or adapted to areas below the draw down limit if permitted by the bathymetrical limits of the species. This seems to be the explanation of the general reduction of herbivorous, big insect larvae as well as the tendency of maximal abundance below the draw down limit for many animals, e.g. *Gammarus lacustris*.

The loss of the macrophytes, combined with the eroding forces, implies a far reaching reduction in the supply of organogenic detritus, the basic food for many components of the fauna. The general reduction of such animal groups as *Chironomidae*, *Oligochaeta*, *Gastropoda*, and *Nematoda*, especially within the regulated area is thus explicable.

The dislocation of the total gastropod fauna, exclusive of *Pulmonata*, to the deeper regions of the littoral in Blåsjön gives an expressive example of an adaptation caused by the regulation. This change in distribution results, however, in quantitative losses which partly can be correlated to a deficit of suitable food. The occurrence of pulmonates even in the profundal regions is established in alpine lakes in Switzerland (ALSTERBERG 1930).

The quantitative increase of the *Hydracarina* in Blåsjön and the high

abundance even within the regulated area of the lake can be explained by the relatively limited reduction of suitable prey (mainly small *Crustacea*), the great mobility for many of them and the general resistance to drying-up in combination with a reduced number of competing animals.

The general tendency towards higher abundance of bottom animals in areas affected by inflows depends mainly on a richer supply of detritus, outdrifted by the running water over adjacent bottoms.

Even in qualitative respect the fauna is richer in areas close to inflows. Among the chironomids the distribution of *Abiskomyia virgo* has already been observed. Furthermore we can mention *Sergentia coracina* Zett., *Microspectra insignilobus* Kieff. and two species of *Stempellinella*, viz. *minor* Edw. and *brevis* Edw., which seem to be entirely restricted to the bottoms influenced by inflows. The great expansion of *Sergentia*, which is reported by STUBE (1958) in the delta of Sannarån after an extensive damming-up has no validity in Blåsjön, among other things owing to the scarcity of organogenic sediments compared with the delta.

The effect of erosion upon the environment

In the bottoms of the regulated region erosion is accelerated by the elimination of the rooted vegetation. The loose material of the bottom is transported to regions below the draw down limit, and the erosion effects an enlargement of the particles of the minerogenic sediments, the final result being a bottom which is uniformly covered with blocks.

After 10 years of regulation Blåsjön exhibits a distinct development in this direction. The bottoms are altogether minerogenic, the particle size decreasing towards greater depth (see p. 190).

The reasons for the distinct limit at the depth of 5 metres have been discussed above, where also the consequences for the fauna have been explained. Here we remind only of the characteristic circumstance that the abundance of *Constempellina brevicosta* and *Abiskomyia virgo* has increased after the regulation. On account of the identical construction of moveable tubes these species are less dependent on the properties of the bottom sediments.

During spring melting water derived from the surrounding shore penetrates between ice and bottom. Below the ice the water collects in runlets and rivulets which continuously increase their eroding force towards deeper regions down to the draw down limit. The running water soon excavates grooves in the loose sediments which rapidly cave in from the edges. Towards greater depths the collection of the melting water into some few larger brooks contributes towards the formation of larger continuous surfaces covered with the fine sediments. This erosion by melting water differs from that by the waves in so far as the size of the particles acted upon increases with growing depth.

As the result of the combined action of the eroding forces the transported

material changes the character of the bottoms below the draw down limit. Under natural conditions these bottoms are characterized by a finely stratified layer of organogenic material at the contact between water and bottom (LIEBMANN 1951). The semi-colloidal surface layer is of special importance. It is formed to a large extent of sinking organic material of planktonic origin. Within the shallower areas the observed washing-out of minerogenic material tears or covers the developed stratification of this organogenic detritus, and hampers all the feeding methods of the fauna. Even in the cases, where the loose surface layer of the bottoms is not completely overlain, e.g. within deep regions, the uniform distribution of the detritus is pierced by minerogenic particles, a condition unfavourable especially to filtrating organisms.

The established reduction of many animal groups (e.g. *Pisidae*, *Chironomidae*) in deeper regions of regulated lakes is to a large extent explicable by these disturbances of the natural stratification of the organogenic material upon the bottoms. As an example we can mention the depression of the upper distribution limit of the chironomid characteristic for these waters, viz. *Heterotrissocladius subpilosus*.

6. Some aspects of the production in regulated and unregulated environments

Even in a regulated lake it might be expected that with increasing distance from the normal environment optimal for the majority of species the biocoenosis becomes poorer in species and more specialized, every species being represented by an increasing number of individuals (the so-called second principle of biocoenology, THIENEMANN, 1950).

For a further discussion the *Chironomidae* are selected to exemplify the situation in Blåsjön. The qualitative results indicate some agreement with the related principle. The number of individuals per species, on the other hand, is less easily explained on the basis of the principles of biocoenology.

The examinations of the bottom fauna result in a continuous determination of the standing crop indicative of the capacity of the different depth zones in different seasons. In general it can be maintained that the density of the populations at different depths is determined by the availability of light, heat, food, and surfaces with suitable sediment. For the study of the capacity of the depth zones with regard to production it is of fundamental importance to know, how much is bound in the food chain of the lake, i.e. the picture has to be completed with the existing interaction between producers and consumers.

In the present case the problem is thus, how much of the energy supplied to the lake in the form of chironomids is bound in the food chain, and what amount of energy is lost from the lake in the form of hatching?

In the bottoms of Ankarvattnet as well as of Blåsjön the areas with the greatest number of species also exhibit the greatest number of individuals in total. This condition is found in the upper littoral of Ankarvattnet, while in Blåsjön it applies to the region immediately below the draw down limit (distribution of larvae and pupae).

The hatching experiments in Ankarvattnet reflect these quantitative conditions. This is, however, not the case in Blåsjön. The standing crop is greatest below the low-water limit, while hatching is most plentiful above this limit. We have here a possibility to study the differences in production dynamics between unregulated and regulated environment. The results show that a higher percentage of the chironomid fauna hatches within the regulated area, in other words that the turnover within the biocoenosis can be assumed to be greater below the draw down limit.

As a preliminary to a more detailed discussion we remind first of the differences existing between the two regions with regard to hatching. Within the regulated area a few or one species only dominate at every depth. As a result we find an irregular course of the hatching with strongly marked maxima of limited duration in comparison with the unregulated zone or the corresponding areas in an unregulated lake. As an example we can mention that within the depth zone 2—4 metres of Blåsjön 90 per cent of the total number of hatching individuals left the bottom within 10 days in 1956, while the corresponding figure was 85 per cent in 1957. The same applies within the zone 5—6 metres, where *Tanytarsus gregarius* during 10 days in 1956 accounted for 85 per cent of the total hatching.

If the chironomid fauna is considered as a production link in the food chain of the lake, it can be assumed that the active consumers are favoured by a supply of chironomids that is rich in species, and at the same time evenly distributed throughout the year. During half of the year the area of regulation is partly or entirely dry, and during the remainder of the year the density of individuals is abnormally low. On this account the concentration of consumers can be assumed to be low. As an example we can mention that the rapacious group Tanypodinae is not encountered within the regulated regions. THIENEMANN (1954) reports, amongst others, larvae of *Tanytarsus* as prey of species of this group.

With regard to the direct connection of the chironomids with the class of consumers at the top of the pyramid of production, viz. the fishes, it can be established that the chironomids are available as prey mainly during the short period of hatching as pupa and imago (NILSSON 1955). In the present case we can assume that the chironomids during a short period of intense hatching restricted to a narrow depth zone (tendency of the species towards stenobathic distribution in Blåsjön) are not available as producers in the same degree as if the same quantity of hatching had been more evenly distributed. It can thus be established that the regulation of Blåsjön has entailed

Table 14. The abundance and bathymetrical distribution of pupae (p.), big larvae (b.l.), and small larvae (s.l.) of *Chironomidae* during different months in the regulated area of Lake Blåsjön. The *Parakiefferiella* generation is in italics. (Individuals per sq.m.)

Depth zone	Jun.	Jul.	Aug.	Sept.	Nov.
0—2 metres					
p.	—	506	13	—	—
b.l.	—	1,100	156	1,304	44
s.l.	95	—	1,043	1,276	22
2—4 metres					
p.	—	172	7	—	—
b.l.	176	1,602	255	418	2,699
s.l.	599	17	1,701	2,992	2,083
4—5 metres					
p.	—	33	15	—	—
b.l.	957	176	73	—	6,190
s.l.	2,354	99	88	—	499
5—6 metres					
p.	120	239	173	—	—
b.l.	2,006	2,721	2,235	1,892	7,568
s.l.	452	242	648	134	1,232

not only a reduction of the wealth of the chironomid fauna in species and individuals; the results indicate moreover a greater loss of energy by hatching in the regulated area than in the unregulated one in that part of the food chain which embraces the main component of the bottom fauna, viz. the chironomids.

Other interactive processes seem to be at work. As an example the conditions within the uppermost zone of 4 metres and its dominant species, *Parakiefferiella bathophila*, are chosen.

From the uniform conditions which exist within this area we are allowed to draw the conclusion that the possible species normally make similar demands, and thus compete with each other in closely related niches, e.g. with regard to food. Under these circumstances the ruling population during early summer can at first be considered as the result of lack of competition by other species, an early species with natural orientation towards the upper littoral, in this case *Parakiefferiella bathophila*, laying hold of all suitable biotopes in the bottom. The growth of the larvae augments the population pressure. This intraspecific competition results in an expansion of the population to areas outside the originally occupied parts of the bottom.

The picture ought to be completed by a consideration of the very limited supply of suitable food within the regulated area which can be supposed also to determine the dimensions of the *Parakiefferiella* population. The supply of food being one of the limiting factors, this species population appears by the growth of its individuals and the general expansion to prevent an occupation by other species. As can be seen from Table 14, a re-

Table 15. The number of hatching individuals/species in Lakes Blåsjön and Ankarvattnet.

Depth zone	Blåsjön		Ankarvattnet	
	number of species		number of species	
2—4 metres	4	15.4	44	11.0
5—6	10	24.1	38	8.1
7—8	20	4.6	28 ¹	5.4 ¹
10—13	11	2.4	14	5.1

¹ Estimated.

newed occupation by small larvae does not take place in the zone of *Parakief-feriella* until after this species has left the bottom as hatching individuals.

The zone of one metre's thickness immediately above the draw down limit forms a transition between the unregulated and the regulated zone. Here the chironomid larvae, especially *Tanytarsini*, can be assumed to survive during winter, and the rapidly increasing number of species points to less extreme environmental conditions.

According to the principles of biocoenology the regulated region of Blåsjön ought to exhibit a great number of individuals per species in comparison with the corresponding regions in Ankarvattnet. The results of the hatchings (Table 15) prove the existence of such an effect which is, however, restricted to the zone of one metre's thickness immediately above the draw down limit. According to the above this effect is, however, partly apparent. The great number of individuals per species can be interpreted as the result of the special conditions within the region 0—6 metres and the occupation of the region by a small number of species which by their high frequency of hatching tend to escape from the food chain. It may be said that in cases in which deficiency of food interacts in the factor complexity the second principle of biocoenology is not applicable.

7. Summary

1. Bottom samples covering an area of 10.8 sq.m. of soft bottom and 7.9 sq.m of block bottom and 369 insect hatching samples have been analysed from the natural Lake Ankarvattnet and the impounded Lake Blåsjön.

2. The water level fluctuations have caused a quantitative reduction of the bottom fauna, in the zone of fluctuations estimated to 70 per cent, in the remaining areas to 25 per cent (Diagr. 6).

3. Maximal abundance of the bottom fauna in the impounded lake is found immediately below the draw down limit (Diagr. 6).

Table 16. Lake *Blåsjön* 1956—1957. The percentages of different species of hatching chironomids/depth zone.

Depth zone 2—4 metres	
<i>Parakiefferiella bathophila</i> KIEFF.	87 %
<i>Constempellina brevicosta</i> EDW.	7
<i>Acricotopus Thienemanni</i> GOETGH.	1
<i>Tanytarsus gregarius</i> EDW.	1
unidentified material	4
Number of species 4. Number of individuals 123	
Depth zone 5—6 metres	
<i>Tanytarsus gregarius</i> EDW.	56
<i>Paratanytarsus hyperboreus</i> BRUND.	19
<i>Paratanytarsus penicillatus</i> GOETGH.	8
<i>Constempellina brevicosta</i> EDW.	6
<i>Psectrocladius fennicus</i> STORÅ.	4
<i>Cricotopus alpicola</i> ZETT.	2
<i>Parakiefferiella bathophila</i> KIEFF.	1
<i>Paracladopelma obscura</i> BRUND.	< 1
<i>Cricotopus</i> sp. lacuum-group	< 1
<i>Stempellinella minor</i> EDW.	< 1
unidentified material	3
Number of species 10. Number of individuals 592	
Depth zone 7—8 metres	
<i>Acricotopus Thienemanni</i> GOETGH.	26
<i>Psectrocladius fennicus</i> STORÅ.	13
<i>Heterotrissocladius Grimshawi</i> EDW.	10
<i>Tanytarsus gregarius</i> EDW.	9
<i>Paratanytarsus penicillatus</i> GOETGH.	8
<i>Parakiefferiella bathophila</i> KIEFF.	5
<i>Tanytarsus heusdensis</i> GOETGH.	5
<i>Cricotopus</i> sp. lacuum-group	3
<i>Constempellina brevicosta</i> EDW.	3
<i>Cricotopus alpicola</i> ZETT.	2
<i>Microspectra groenlandica</i> ANDERS.	1
<i>Paracladopelma obscura</i> BRUND.	1
<i>Procladius</i> sp.	1
<i>Diamesa</i> sp.	1
<i>Paratanytarsus hyperboreus</i> BRUND.	1
<i>Ablabesmyia</i> spp.	1
<i>Monodiamesa bathyphila</i> PAG.	< 1
<i>Tanytarsus curticornis</i> KIEFF.	< 1
<i>Protanypus morio</i> ZETT.	< 1
unidentified material	8
Number of species 20. Number of individuals 209	
Depth zone 8—10 metres	
<i>Acricotopus Thienemanni</i> GOETGH.	34
<i>Microspectra groenlandica</i> ANDERS.	24
<i>Cricotopus</i> sp. lacuum-gr.	10
<i>Procladius</i> sp.	8
<i>Paratanytarsus penicillatus</i> GOETGH.	4
<i>Constempellina brevicosta</i> EDW.	4
<i>Tanytarsus gregarius</i> EDW.	2
<i>Parakiefferiella bathophila</i> KIEFF.	2
<i>Cricotopus alpicola</i> ZETT.	2
<i>Diamesa</i> sp.	2
<i>Heterotanytarsus apicalis</i> KIEFF.	2
<i>Protanypus caudatus</i> EDW.	2
unidentified material	4
Number of species 12. Number of individuals 50	

Table 16. Continued.

Depth zone 10—13 metres	
<i>Microspectra groenlandica</i> ANDERS.	29
<i>Aricotopus Thienemanni</i> GOETGH.	18
<i>Constempellina brevicosta</i> EDW.	14
<i>Heterotrissocladius Määri</i> BRUND.	8
<i>Paratanytarsus penicillatus</i> GOETGH.	8
<i>Cricotopus alpicola</i> ZETT.	7
<i>Abiscomyia virgo</i> EDW.	3
<i>Heterotrissocladius Grimshawi</i> EDW.	3
<i>Ablabesmyia</i> sp.	3
<i>Procladius</i> sp.	2
<i>Diamesa</i> sp.	2
unidentified material	3
Number of species 11. Number of individuals 65	
Depth zone 13—20 metres	
<i>Microspectra groenlandica</i> ANDERS.	60
<i>Aricotopus Thienemanni</i> GOETGH.	18
<i>Heterotrissocladius subpilosus</i> EDW.	14
<i>Tanytarsus lugens</i> KIEFF.	8
Number of species 4. Number of individuals 50	

4. Great quantitative changes have occurred in the balance between the different groups of bottom animals, involving an increased share of *Chironomidae* and a decrease of benthonic *Crustacea*, the *Oligochaeta* being indifferent (Table 3).

5. Animals being dependent on an intact littoral zone are heavily reduced, for instance *Gammarus lacustris* and many insect larvae (Diagr. 14 and 15).

6. Some groups of animals, e.g. *Gastropoda*, that have been almost eliminated in the depth zone normally comprising optimal habitat conditions have increased in abundance within new areas below the draw down limit (Diagr. 19).

7. The reduction of filtrating organisms below the draw down limit even in the profundal regions is suggested to depend on the disturbance of the stratifications in bottom surface layers, caused by minerogenic material eroding from the regulated area (*Pisidae* and *Chironomidae*: Diagr. 11).

8. The changed balance within the *Chironomidae* involving increased percentage of the main groups *Tanytarsini* and *Orthoclaadiinae* and heavy reductions of *Chironomini* is suggested to depend on lowered temperature standard in the bottoms of the entire littoral and upper profundal (Table 7 and 9).

9. The bathymetrical distribution of the main chironomid groups in the natural lake is compared with the occurrence of these groups in lakes at different altitudes. The two phenomena may be understood on the basis of the environmental requirements of the chironomid types in question. The natural orientation of *Orthoclaadiinae* and *Tanytarsini* towards the upper littoral is accentuated in the regulated lake (Table 8 and 9).

10. As a result of the general reduction of chironomid species, the periods

Table 17. Lake Ankarvattnet. The percentages of the different species of hatching chironomids/depth zone.

Depth zone 2—4 metres	
<i>Parakiefferiella bathophila</i> KIEFF.	27 0/0
<i>Polypedilum albicorne</i> MEIG.	9
<i>Microcricotopus bicolor</i> EDW.	6
<i>Corynoneura cleripes</i> WINN.	3
<i>Cricotopus albiforceps</i> KIEFF.	3
<i>Cricotopus alpicola</i> ZETT.	3
<i>Tanytarsus heusdensis</i> GOETGH.	3
<i>Stempellinella brevis</i> EDW.	3
<i>Tanytarsus telmaticus</i> LINDBERG.	3
<i>Heterotrissocladius marcidus</i> EDW.	2
<i>Psectrocladius calcaratus</i> EDW.	2
<i>Ablabesmyia</i> spp. (3 species)	2
<i>Trissocladius conformis</i> EDW.	2
<i>Psectrocladius fennicus</i> STORÅ.	2
<i>Heterotanytarsus apicalis</i> KIEFF.	2
<i>Constempellina brevicosta</i> EDW.	2
<i>Tanytarsus curticornis</i> KIEFF.	2
<i>Corynoneura scutellata</i> WINN.	2
<i>Orthocladius consobrinus</i> HOLMGR.	1
<i>Cricotopus</i> sp. lacuum-group	1
<i>Stempellinella minor</i> EDW.	< 1
<i>Tanytarsus</i> cf. <i>separabilis</i> BRUND.	< 1
<i>Cricotopus bilobatus</i> STOR.	< 1
<i>Heterotrissocladius Grimshawi</i> EDW.	< 1
<i>Eudactylocladius mixtus</i> HOLMGR.	< 1
<i>Procladius barbatus</i> BRUND.	< 1
<i>Cryptochironomus</i> sp.	< 1
<i>Chironomini</i> sp. 1	< 1
<i>Microtendipes brevitarsis</i> BRUND.	< 1
<i>Acricotopus Thienemanni</i> GOETGH.	< 1
<i>Microspectra groenlandica</i> ANDERS.	< 1
<i>Trissocladius</i> sp.	< 1
<i>Prodiamesa olivacea</i> MEIG.	< 1
<i>Metriocnemus</i> sp. <i>hygropetricus</i> -group	< 1
<i>Paracladopelma obscura</i> BRUND.	< 1
<i>Chironomini</i> sp. 2	< 1
<i>Psectrocladius sordidellus</i> EDW.	< 1
<i>Paratanytarsus penicillatus</i> GOETGH.	< 1
<i>Psectrocladius Zetterstedti</i> BRUND.	< 1
<i>Cricotopus</i> sp.	< 1
<i>Chironomini</i> sp. 3	< 1
unidentified material	14
Number of species 44. Number of individuals 485	
Depth zone 5—6 metres	
<i>Parakiefferiella bathophila</i> KIEFF.	16
<i>Tanytarsus telmaticus</i> LINDBERG.	16
<i>Trissocladius conformis</i> EDW.	9
<i>Stempellinella minor</i> EDW.	5
<i>Tanytarsus curticornis</i> KIEFF.	5
<i>Microspectra insignilobus</i> KIEFF.	5
<i>Sergentia coracina</i> ZETT.	4
<i>Psectrocladius fennicus</i> STORÅ.	4
<i>Heterotanytarsus apicalis</i> KIEFF.	4
<i>Ablabesmyia</i> spp. (3 species)	3
<i>Acricotopus Thienemanni</i> GOETGH.	3
<i>Orthocladius consobrinus</i> HOLMGR.	3
<i>Heterotrissocladius Grimshawi</i> EDW.	2
<i>Microspectra groenlandica</i> ANDERS.	2

Table 17. Continued.

<i>Parachironomus</i> cf. <i>spissatus</i> BRUND.	2
<i>Polypedilum pullum</i> ZETT.	1
<i>Polypedilum albicorne</i> MEIG.	1
<i>Psectrocladius calcaratus</i> EDW.	1
<i>Corynoneura scutellata</i> WINN.	1
<i>Microcricotopus bicolor</i> ZETT.	1
<i>Cryptochironomus</i> sp.	1
<i>Protanypus morio</i> ZETT.	< 1
<i>Procladius</i> sp. I+II	< 1
<i>Tanytarsus heusdensis</i> GOETGH.	< 1
<i>Tanytarsus</i> cf. <i>separabilis</i> BRUND.	< 1
<i>Stempellinella brevis</i> EDW.	< 1
<i>Cricotopus</i> sp. <i>lacuum</i> -group	< 1
<i>Trissocladius</i> sp.	< 1
<i>Microtendipes brevitarsis</i> BRUND.	< 1
<i>Metriocnemus</i> sp. <i>hygropectricus</i> -group	< 1
<i>Cricotopus</i> sp.	< 1
<i>Stichtochironomus</i> sp.	< 1
<i>Chironomus connectens</i>	< 1
<i>Corynoneura cleripes</i> WINN.	< 1
unidentified material	4
Number of species 38. Number of individuals 309	
Depth zone 10—13 metres	
<i>Acricotopus Thienemanni</i> GOETGH.	23
<i>Cricotopus</i> sp. <i>alpicola</i> -group	23
<i>Microspectra groenlandica</i> ANDERS.	20
<i>Tanytarsus lugens</i> KIEFF.	7
<i>Parakiefferiella bathophila</i> KIEFF.	7
<i>Heterotrissocladius Grimshawi</i> EDW.	4
<i>Chironomini</i> sp. 1	3
<i>Psectrocladius fennicus</i> STORÅ.	3
<i>Microtendipes brevitarsis</i> BRUND.	1
<i>Ablabesmyia</i> sp.	1
<i>Chironomini</i> sp. 4	1
<i>Cryptochironomus</i> sp.	1
<i>Procladius</i> sp. III	1
<i>Heterotanytarsus apicalis</i> KIEFF.	1
unidentified material	4
Number of species 14. Number of individuals 71	

of emergence are limited to a few heavy concentrations especially within the regulated area. The emergence maximum normally occurring in natural lakes during spring is almost eliminated in the whole littoral (Diagr. 8).

11. The increased abundance of *Cladocera* that follows the first years of damming up has 10 years after the start of regulation ceased, and moreover as an effect of the continuous erosion decreased in abundance (Diagr. 15).

12. There is a general tendency towards higher abundance of bottom animals in the vicinity of inflows, which is supposed to depend on a combined effect of outdrifted animals and a richer supply of nutrients in these areas.

13. A special study was carried out on the temperature conditions in bottoms affected by drainage and freezing during the draw down period. Of the animals from the frozen-in bottoms 80 per cent of the individuals were alive (Diagr. 21, Table 13).

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The effect of water-level fluctuations on the feeding habits of trout and char in the Lakes Blåsjön and Jormsjön, North Sweden

By NILS-ARVID NILSSON

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1. Introduction

Investigations into the feeding habits of trout and char in Blåsjön have been continued during the years 1944, 1945, 1946, 1949, 1954, 1955, 1956, and 1959. The sampling has been carried out mainly with gill-nets of a certain mesh-size distribution (cf. NILSSON 1955). The situation of the fishing stations can be seen in the map, Fig. 1. The material, which in part has been presented earlier (NILSSON 1955 a, b, 1959, 1960), now includes the following number of samples:

	Year	Number of trout	Char
Before regulation ¹	1944	69	32
	1945	35	46
	1946	213	291
After regulation	1949	172	198
	1954	170	243
	1955	27	27
	1956	39	71
	1959	100	148
Sum		825	1,056

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

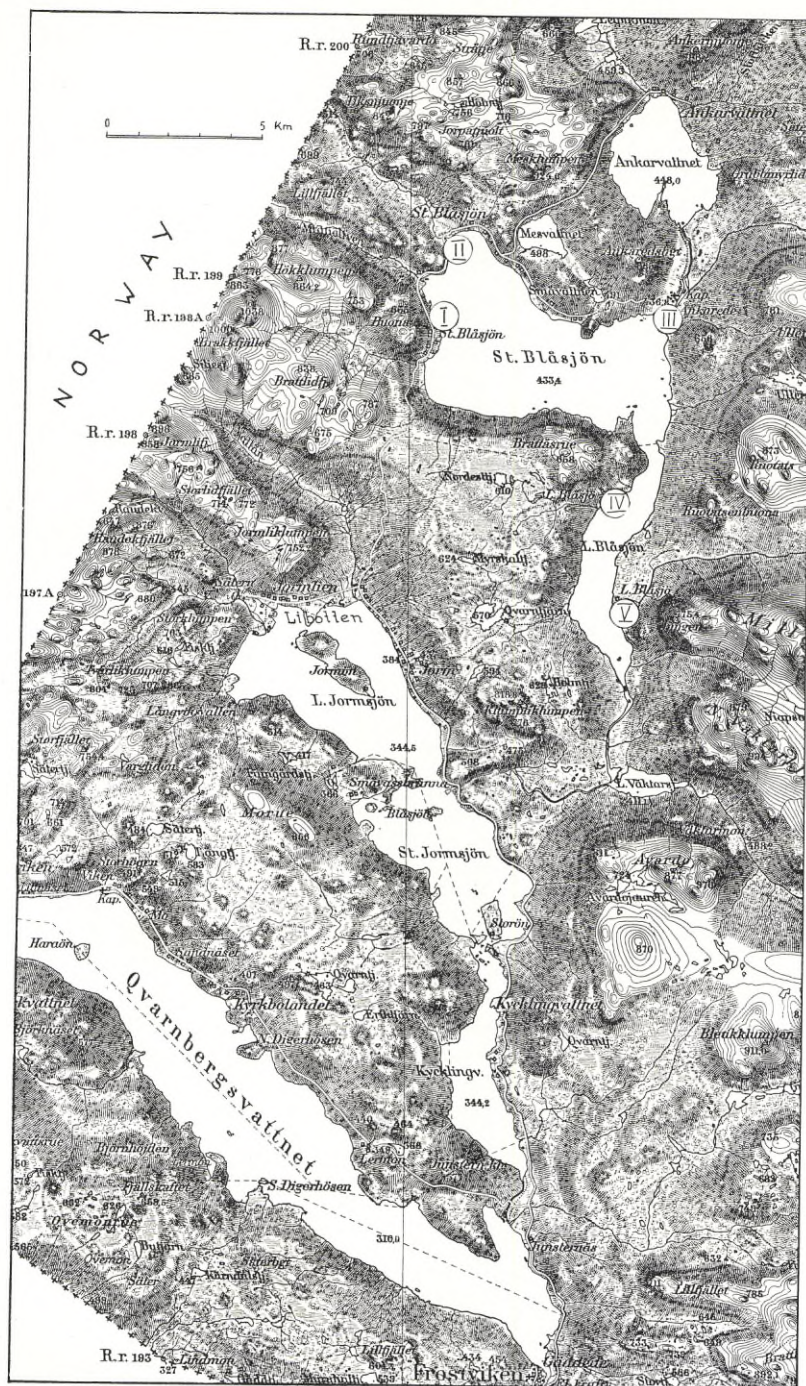


Fig. 1. Map of the investigated lakes. Figures indicate fishing stations.

In Jormsjön, where similar investigations have been carried out during the years 1944, 1945, 1946, 1947, 1955, and 1956, the material includes the following number of samples:

	Year	Number of trout	Char
Before regulation	1944	49	55
	1945	39	66
	1946	65	138
	1947	—	38
After regulation	1955	49	73
	1956	25	28
Sum		227	398

In connection with the investigations in Blåsjön the nearby unregulated Lake Ankarvattnet was examined during the years 1944, 1945, and 1959.

The figures underlying the following description have been obtained in the way described by NILSSON (1955, p. 163) as "volumetric" values (mean percentage of stomach volume).

For details in the general physical and biotic conditions of Blåsjön and Ankarvattnet the reader is referred to GRIMÅS (1961).

2. The effect of the water-level fluctuations on the prey fauna

In close connection with the investigation into the ecology of the fish the invertebrate fauna of Blåsjön has been studied (MÄÄR, unpublished, GRIMÅS 1959, 1960 a, 1961).

The regulation of water-level for hydro-electric storage purposes started to full extent in the year 1949. After that time the water-level has fluctuated from 436 metres above sea-level (normal 434 m) in summer to 430 m in winter. In 1959 the lake was drawn down to 427 metres above sea-level (amplitude 9 m).

The changes within the prey fauna have occurred in Blåsjön and Jormsjön mainly as in other examined lakes with similar water-level fluctuations (cf. DAHL 1926, 1932, HUITFELDT-KAAS 1935, RUNNSTRÖM 1946, 1951, 1952, CUERRIER 1954, RODHE *et alii* 1957, NILSSON 1958, QUENNERSTEDT 1958, RAWSON 1958, STUBE 1958, MILLER and PAETZ 1959, AASS 1960, AXELSSON 1961, GRIMÅS and NILSSON 1961). The characteristic features are the following:

1) Due to the damming-up new minerogenic and organogenic material is brought to the lake during the first years of regulation. This results in an increased primary production (RODHE *et al.* 1957), and moreover makes different terrestrial animals available as fish food. It is also probable that the decreased discharge at the outlet of the lake implies a decreased escape of

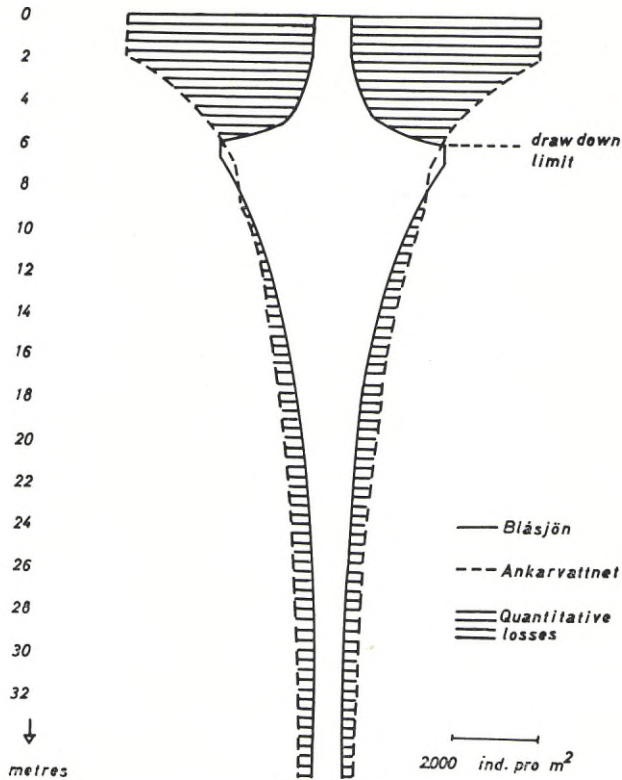


Fig. 2. The vertical distribution of the bottom fauna of Blåsjön compared to Ankarvattnet (After GRIMÅS 1961).

plankton (AXELSSON 1961). This positive effect of the damming-up results in an increased growth rate of the fish in the course of the first years after the start of the regulation (RUNNSTRÖM 1951, FROST 1956). The intensity and duration of this effect varies widely from lake to lake. It is not known, whether after the cessation of the damming-up effect primary production returns to the intensity it had before the start of regulation.

2) As a result of the higher water-level during the vegetative periode the change in light conditions brings about an upward shifting of the lower limit of the rooted vegetation (QUENNERSTEDT 1958). This has consequences for the fauna that is bound to the vegetation. GRIMÅS (1961) has calculated the reduction of the bottom fauna below the draw-down limit to 25 per cent.

3) Through a combined effect of drying up, freezing, an erosion first the aquatic vegetation then the fine-grained sediments disappear from the zone exposed to water-level fluctuations, this zone becoming increasingly uniform and sterile. The entire bottom fauna within this zone is reduced to 70 per cent. Above all the bigger crustaceans (100 per cent), major insect larvae and nymphs (80 per cent), and molluscs are severely affected (GRIMÅS 1961).

4) The heat budget of the water is altered towards more arctic conditions,

Table 1. The feeding habits of trout and char in Jormsjön before water-level regulation.

	Trout				Char					
	1944 July	1945 Aug.	1945 Oct.	1946 Aug.	1944 July	1945 Aug.	1945 Oct.	1946 Aug.	1946 Sept.	1947 Jan.
Fish	—	5.6	100.0	—	—	3.3	—	—	—	—
Spawn	—	—	—	—	—	—	45.2	—	17.8	—
<i>Phyllopora</i> , indet.	—	—	—	1.7	25.0	—	—	62.9	28.2	—
<i>Daphnia</i>	—	—	—	7.9	—	9.0	23.6	—	—	—
<i>Bosmina</i>	—	—	—	—	3.8	—	—	—	—	6.7
<i>Bythotrephes</i>	—	—	—	—	—	9.3	7.4	—	—	—
<i>Eurycercus</i>	—	24.2	—	—	16.1	34.3	10.5	7.2	1.3	—
<i>Cyclops</i>	—	—	—	—	—	—	—	—	—	20.0
<i>Heterocope</i>	—	—	—	—	—	—	—	—	50.3	—
<i>Gammarus</i>	4.5	17.0	—	11.5	1.3	5.7	3.5	—	1.1	18.1
<i>Asellus</i>	17.6	45.9	—	11.5	18.1	36.8	9.8	2.5	—	39.5
<i>Limnaea</i>	6.8	0.4	—	5.2	7.3	—	—	—	0.1	—
<i>Planorbis</i>	—	2.0	—	0.8	—	—	—	—	—	—
<i>Pisidium</i>	—	—	—	0.1	—	0.4	—	0.1	—	—
<i>Sphaerium</i>	—	—	—	—	0.1	—	—	—	—	—
<i>Oligochaeta</i>	1.0	—	—	—	—	—	—	—	—	—
<i>Trichoptera l.</i>	31.0	4.4	—	21.9	1.2	—	—	0.3	—	10.0
<i>Ephemeroptera l.</i>	7.7	—	—	11.7	9.7	—	—	10.2	—	0.7
<i>Plecoptera l.</i>	0.4	0.5	—	2.2	—	—	—	3.4	—	3.3
<i>Sialis l.</i>	—	—	—	0.1	—	—	—	—	—	—
<i>Odonata l.</i>	—	—	—	—	—	0.3	—	—	—	—
<i>Dytiscidae l.</i>	0.1	—	—	—	0.3	—	—	—	—	—
<i>Chironomidae l.</i>	1.2	—	—	2.7	9.6	0.5	—	0.1	—	1.7
<i>Simuliidae l.</i>	1.0	—	—	—	—	—	—	—	—	—
<i>Tipulidae l.</i>	2.1	—	—	0.1	—	—	—	—	—	—
<i>Trichoptera p.</i>	—	—	—	3.5	—	—	—	—	—	—
<i>Chironomidae p.</i>	5.2	—	—	—	0.8	—	—	—	—	—
<i>Trichoptera i.</i>	0.4	—	—	—	0.1	0.2	—	11.4	—	—
<i>Ephemeroptera i.</i>	0.2	—	—	—	—	—	—	—	—	—
<i>Chironomidae i.</i>	11.7	—	—	—	0.7	—	—	1.0	1.2	—
<i>Tipulidae i.</i>	3.6	—	—	16.7	2.9	—	—	—	—	—
Terr. insects	5.5	—	—	1.9	2.9	—	—	0.9	—	—
<i>Nostoc</i> and other plants	—	—	—	0.5	0.1	—	—	—	—	—
Miscellaneous	—	—	—	—	—	0.2	—	—	—	—

comprising changes in the specific composition of the prey fauna (e.g. the main tribe of *Chironomini* among the chironomids disappears in favour of *Tanytarsini*) (GRIMÅS 1961).

5) The most important remaining prey species are the chironomids, tipulids, and the cladocere *Eurycercus lamellatus*. The number of chironomid species is heavily reduced so that the very important emergence maximum in June practically disappears (GRIMÅS 1961).

6) The most important refuges with remaining prey fauna are found in the vicinity of the river inlets (STUBE 1958, GRIMÅS 1961).

The reduction of the entire bottom fauna of Blåsjön is illustrated by Figure 2.

Table 2. The food of trout in Blåsjön 1959 (average June—October).
Comparison between fishing stations.

	Station				
	I	II	III	IV	V
Fish	6.7	—	1.7	6.3	16.7
<i>Bythotrephes</i>	—	—	—	1.0	—
<i>Daphnia</i>	—	4.5	—	1.6	—
<i>Holopedium</i>	—	4.0	—	—	—
<i>Eurycercus</i>	12.7	21.7	—	12.3	8.3
<i>Limnaea</i>	4.5	5.0	—	—	—
<i>Planorbis</i>	0.1	—	—	—	12.5
<i>Trichoptera l.</i>	0.1	8.0	45.5	8.3	9.6
<i>Ephemeroptera l.</i>	4.0	5.1	16.9	10.5	10.5
<i>Plecoptera l.</i>	10.2	5.8	4.2	—	2.1
<i>Dytiscidae l.</i>	0.4	—	—	—	—
<i>Chironomidae l.</i>	3.7	12.1	1.2	2.0	2.1
<i>Ceratopogonidae l.</i>	1.2	—	—	—	—
<i>Tipulidae l.</i>	6.2	6.3	2.2	0.6	—
<i>Trichoptera p.</i>	0.2	—	0.3	—	—
<i>Chironomidae p.</i>	4.7	—	—	—	—
<i>Ceratopogonidae p.</i>	0.4	—	—	—	—
<i>Trichoptera i.</i>	—	1.8	0.3	0.3	—
<i>Ephemeroptera i.</i>	0.3	1.0	1.2	0.7	—
<i>Dytiscidae i.</i>	—	0.8	0.2	0.2	7.1
<i>Chironomidae i.</i>	5.4	1.0	1.4	0.3	—
<i>Tipulidae i.</i>	2.8	3.0	10.3	32.1	7.0
<i>Empididae i.</i>	0.3	—	—	—	—
Terr. insects	36.2	20.2	14.4	24.0	24.2

Also Jormsjön first became regulated in the year 1949. The regulation implies a draw down to 343.8 metres above sea-level and a damming up to 346.5 m. These fluctuations have not been great enough to eliminate certain of the more important prey species (e.g. *Gammarus*, *Asellus*). On account of the topography, special conditions were found within a shallow area called "Libotten" (cf. map) characterized by a bar of sand built up by a rivulet that impounds the whole area. Within the impounded area an important part of the sediments has been preserved for the benefit of the fauna that within this area is more abundant than in other parts of the regulation zone of Jormsjön or Blåsjön (GRIMÅS 1960 b).

3. The feeding habits of the fish in Blåsjön before water-level regulation

Since extensive reports on the feeding habits of fish before the regulation of Blåsjön have been published earlier (NILSSON 1955 b, 1960) only a brief characterization will be given here.

During spring and early summer both trout and char preyed on food originating mainly from the bottoms. Especially trout were then bound to

Table 3. The food of char in Blåsjön 1959 (average June—October).
Comparison between fishing stations.

	Station				
	I	II	III	IV	V
Fish	—	1.1	—	—	—
<i>Bythotrephes</i>	0.6	0.1	—	7.2	—
<i>Daphnia</i>	22.6	50.5	21.4	36.8	6.6
<i>Bosmina</i>	1.5	2.9	25.6	0.9	2.5
<i>Holopedium</i>	0.3	0.3	—	18.2	65.6
<i>Eurycercus</i>	47.1	27.3	10.3	36.8	7.2
<i>Heterocope</i>	2.4	8.4	6.9	—	2.5
<i>Ephemeroptera l.</i>	0.5	+	0.3	—	6.3
<i>Plecoptera l.</i>	2.2	0.4	4.3	—	—
<i>Chironomidae l.</i>	0.6	—	14.4	—	—
<i>Chironomidae p.</i>	0.6	—	0.8	—	—
<i>Plecoptera i.</i>	—	—	2.5	—	—
<i>Chironomidae i.</i>	0.7	—	—	—	—
<i>Tipulidae i.</i>	—	0.4	—	—	—
Terr. insects	20.8	8.7	13.1	—	9.4

the uppermost parts of the litoral. Important foods for both species were the amphipod *Gammarus lacustris* SARS, the molluscs *Limnaea peregra* (MÜLLER) and *Planorbis (Gyraulus)* sp., larvae of the ephemerid *Siphonurus lacustris* EATON and the plecoptera *Nemoura avicularis* MORTON, pupae and imagines of many species of chironomids, e.g. *Ablabesmyia* spp., *Procladius* sp., *Heterotrissocladius* spp., *Psectrocladius* sp., and imagines of *Tipula* sp. The predominant food of trout were during all seasons trichoptera larvae, mostly *Phryganea obsoleta* HAGEN, *Apatania* sp. and *Polycentropus* sp.

During the course of late summer and autumn char were to a growing extent feeding on small crustaceans (cf. NILSSON 1960). The predominant species were *Bosmina coregoni* BAIRD (July—August), *Daphnia longispina* LEYDIG (August—September), *Holopedium gibberum* ZADDACH (October), *Eurycercus lamellatus* (O. F. MÜLLER) (August—September), and *Heterocope saliens* LILLJEB. (September).

In Blåsjön there are at least two separate populations of char (MÄÄR 1949). Of these one is distinguished by dwelling in very deep water (spawning at about 100 m) and by having a very slow growth rate. These so called "deep char" may feed mainly on small crustaceans.

4. The feeding habits of the fish in Jormsjön before water-level regulation

The feeding habits of trout and char in Jormsjön before regulation are shown in Table 1.

A comparison with the corresponding situation in Blåsjön reveals important similarities. Thus during summer char fed mainly on planktonic or half

Table 4. The food of trout in Blåsjön 1959 (average June—November).
Variation between size classes (total length).

	125—200	201—250	251—300	> 301
Fish (char)	4.6	1.8	8.9	22.2
<i>Bythotrephes</i>	—	0.6	—	—
<i>Daphnia</i>	—	2.5	+	—
<i>Holopedium</i>	—	1.4	—	—
<i>Eurycerus</i>	21.3	8.1	3.6	—
<i>Limnaea</i>	4.2	2.0	—	—
<i>Planorbis</i>	3.5	—	—	—
Trichoptera l.	16.3	5.2	18.8	36.7
Ephemeroptera l.	9.1	8.1	13.4	—
Plecoptera l.	6.1	8.8	2.0	—
Dytiscidae l.	0.2	0.2	—	—
Chironomidae l.	2.3	5.0	3.6	5.6
Ceratopogonidae l.	0.1	0.8	—	—
Tipulidae l.	4.0	2.0	6.5	2.2
Trichoptera p.	0.2	0.2	—	—
Chironomidae p.	0.7	1.5	—	11.1
Trichoptera i.	0.6	0.3	0.4	—
Ephemeroptera i.	1.0	0.6	0.4	—
Dytiscidae i.	0.6	1.5	0.1	—
Chironomidae i.	3.0	0.9	—	—
Tipulidae i.	5.5	16.0	12.8	8.3
Empididae i.	—	0.2	—	—
Terr. insects	16.8	32.4	29.6	13.9

benthic phyllopo­ds and copepods (*Daphnia longispina*, *Bosmina coregoni*, *Bythotrephes longimanus*, *Eurycerus lamellatus*, *Heterocope saliens*, etc.), and the preference of trout for trichoptera larvae is obvious also in this lake. A very important difference in relation to Blåsjön, however, was the very significant exploitation of the isopod *Asellus aquaticus* which in Jormsjön seems to have taken the place of *Gammarus lacustris* in Blåsjön.

5. The feeding habits of the fish in Blåsjön after water-level regulation

Before the influence of the regulation upon the composition of the food of the fish is treated, something ought to be said about the variations in feeding habits caused by differences between fishing stations and between size classes of fish. The samples from 1959 have been used as an example.

Variations between fishing stations

Five fishing stations were used (cf. map, Fig. 1). Station I, "Södra Blåsjön", is the only one representing an environment that is maximally affected by water-level regulation, characterized by sterile block, gravel, and sandy

Table 5. The food of char in Blåsjön 1959 (average June—October).
Variation between size-classes (total length).

	125—200	201—250	251—300	> 301
Fish	2.8	—	—	—
<i>Bythotrephes</i>	—	—	0.2	7.0
<i>Bosmina</i>	17.9	1.2	1.5	1.7
<i>Daphnia</i>	24.3	50.7	28.8	13.0
<i>Holopedium</i>	9.7	10.1	2.4	—
<i>Eurycercus</i>	29.0	22.5	37.4	36.9
<i>Heterocope</i>	1.1	3.9	13.5	4.0
<i>Ephemeroptera l.</i>	—	1.2	0.1	1.5
<i>Plecoptera l.</i>	0.6	1.8	0.8	—
<i>Chironomidae l.</i>	3.1	1.5	0.6	1.5
<i>Chironomidae p.</i>	0.4	—	0.5	—
<i>Chironomidae i.</i>	—	—	0.6	—
<i>Tipulidae i.</i>	—	—	1.5	0.3
Terr. insects	11.1	7.1	12.0	33.7

bottoms down to the draw-down limit. All other stations are more or less influenced by running water. The Stations II, III, and V are inlet areas, Station IV is influenced by running water because of the strong current through the eastern part of Blåsjön. Tables 2 and 3 give the impression of an important differences between the stations of which, however, not all could be ascribed to environmental differences. A significant difference seems to exist between the consumption of trichoptera larvae at Station I and the remaining stations. This could be explained by the preserving effect of running water upon the species consumed (*Apatania* sp. and *Agraylea* sp.) (Table 2).

Variations between size classes

Tables 4 and 5 suggest a certain difference in feeding habits between fish of different size, with the well-known correlation big fish — big food objects, etc. (cf. e.g. LINDSTRÖM 1955, NILSSON 1955). As to trout a tendency for big fish to eat other fish, for smaller fish to eat *Eurycercus* is obvious. When the prey fish could be identified they were mostly found to have been char (probably one year old).

In the case of char small fish exhibit an obvious tendency to feed on the smallest crustaceans (*Bosmina*), while bigger fish prefer bigger crustaceans (*Eurycercus* and *Bythotrephes*). A tendency for bigger fish to prefer surface food (*Tipulidae*, terrestrial insects) could also be discerned.

Comparison between the feeding habits in different years

With the aim of forming an idea of in what way the regulation has influenced the feeding habits of the fish two methods have been used. 1) The changes from year to year have been noted from 1944, i.e. five years before the

Table 6. The percentage of *Gammarus lacustris* in the food of trout (T) and char (C) in Blåsjön.

		1944	1945	1946	1949	1954	1955	1956	1959
May-June	T	—	—	0.1	29.2	15.3	—	—	0.0
	C	—	—	3.6	32.4	4.3	—	—	0.0
July	T	3.9	—	7.9	7.7	4.9	—	0.2	0.0
	C	7.8	—	20.4	2.3	2.2	—	0.1	0.0
August	T	—	14.1	3.6	1.3	6.0	0.1	0.8	0.0
	C	—	6.2	1.5	3.3	1.2	4.9	—	0.0
September	T	—	—	22.1	5.1	0.4	—	—	0.0
	C	—	—	31.7	3.8	0.7	—	—	0.0
October	T	—	—	42.3	13.1	—	—	—	0.0
	C	—	—	19.2	4.6	1.8	—	—	0.0

start of regulation, to 1959, i.e. ten years after the start of regulation. Moreover 2) the feeding of the fish in the nearby unregulated Lake Ankarvattnet has been compared with a corresponding fishing station in Blåsjön.

A comparison of the composition of the food in different years convincingly shows that the part played by the bottom fauna as a whole has decreased essentially after the start of regulation. This tendency is most obvious in the case of char, but is quite noticeable also in the case of trout. The decrease is gradual, less ten years after the start of regulation the bottom situation seems to have been reached (cf. e.g. CUERRIER 1954, GRIMÅS 1961).

A splitting-up the bottom-food in its most important components shows that not all groups of animals have been hit by the water-level fluctuations in an equally severe way. The severest damage seems to have been experienced by the amphipod *Gammarus lacustris* which was very important before the start of regulation, but had nearly disappeared already after six—seven years (cf. Table 6 and Fig. 3).

Also the molluscs *Limnaea* and *Planorbis* have entirely disappeared from the diet of char, but still play a certain part in the food of trout (Table 7).

Table 7. The percentage of *Mollusca* in the food of trout and char in Blåsjön.

		1944	1945	1946	1949	1954	1955	1956	1959
May-June	T	—	—	0.0	0.2	3.6	—	—	6.4
	C	—	—	1.7	0.3	2.4	—	—	0.0
July	T	4.3	—	6.6	10.7	6.1	—	7.9	0.0
	C	21.6	—	14.0	5.4	5.7	—	2.6	0.0
August	T	—	13.4	9.1	4.0	19.8	1.2	1.1	6.2
	C	—	6.0	14.6	3.2	0.0	3.1	—	0.0
September	T	—	—	12.7	6.0	2.9	—	—	0.1
	C	—	—	5.4	0.0	0.0	—	—	0.0
October	T	—	—	18.1	7.1	—	—	—	0.0
	C	—	—	4.9	0.2	6.6	—	—	0.0

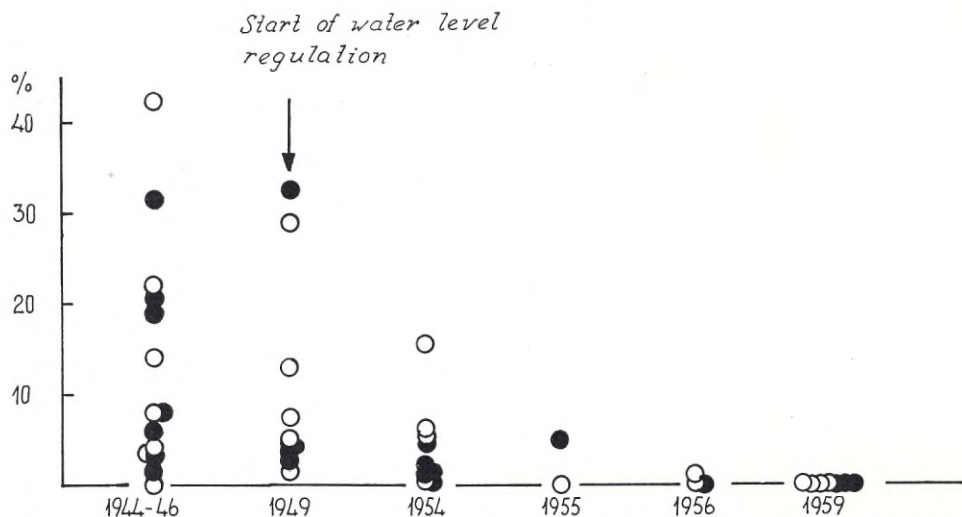


Fig. 3. The percentage of *Gammarus lacustris* in the food of trout and char in Blåsjön (monthly figures). Trout=white dots, char=black dots.

Of a special importance are the changes that have occurred in the trout's consumption of trichoptera which before the start of regulation were the main food of this species. Table 8 gives the impression that the exploitation of this food during the last years has decreased. This tendency applies especially to the months June—August. Moreover, the consumption has changed from big species (*Phryganea obsoleta*) to smaller ones (*Apatania* sp. and *Agraylea* sp.). The latter species is bound to some small areas with rests of vegetation that occur in the vicinity of running water (GRIMÅS 1961). The high figure for October 1959 is in part due to trout caught in the vicinity of the mouth of the River Ankarälven (cf. Table 2).

The exploitation of the rest of the bigger aquatic insects (*Ephemeroptera*,

Table 8. The percentage of *Trichoptera* (larvae, pupae, and imagines) in the food of trout and char in Blåsjön.

		1944	1945	1946	1949	1954	1955	1956	1959
May-June	T	—	—	29.3	22.4	32.0	—	—	0.0
	C	—	—	0.0	5.5	0.2	—	—	0.0
July	T	25.8	—	36.1	45.8	11.9	—	20.5	0.0
	C	4.7	—	8.7	3.8	0.9	—	2.7	0.0
August	T	—	21.8	24.5	59.9	33.4	7.5	5.6	0.8
	C	—	0.0	10.4	1.1	2.2	3.3	—	0.0
September	T	—	—	33.0	30.7	2.6	—	—	11.1
	C	—	—	3.2	0.6	0.0	—	—	0.0
October	T	—	—	39.1	60.9	32.0	—	—	41.9
	C	—	—	< 0.1	0.0	0.0	—	—	0.0

Table 9. The percentage of *Ephemeroptera* (E), *Plecoptera* (P), *Sialis* (S), and *Dytiscidae* (D) in the food of trout and char in Blåsjön. Brackets include dominant food item.

		1944	1945	1946	1949	1954	1955	1956	1959
May—June	T	—	—	43,6 (P)	33,1 (P)	9,2 (D)	—	—	4,1 (P)
	C	—	—	89,2 (P)	4,2 (P)	0,6 (D)	—	—	2,2 (E)
July	T	8,2 (E)	—	25,8 (E)	5,1 (D)	15,5 (E)	—	13,0 (E)	33,2 (E)
	C	3,1 (E)	—	9,5 (E)	0,0	2,5 (E)	—	0,1 (D)	5,0 (E)
August	T	—	18,5 (E)	14,4 (E)	10,7 (E)	11,7 (E)	34,0 (E)	10,8 (E)	16,3 (E)
	C	—	0,0	11,1 (E)	0,2 (E)	5,6 (E)	15,4 (E)	—	0,0
September	T	—	—	4,9 (P)	9,5 (E)	0,0	—	—	7,8 (E)
	C	—	—	2,3 (P)	0,2 (E)	0,0	—	—	0,0
October	T	—	—	0,2 (P)	0,1 (D)	0,0	—	—	12,6 (P)
	C	—	—	0,1 (P)	0,1 (S)	0,4 (S)	—	—	1,8 (P)

Plecoptera, and *Dytiscidae*) does not seem to have changed significantly (Table 9). The predominant species before and after regulation have been the ephemerid *Siphonurus lacustris* and *Nemoura avicularis*.

GRIMÅS' investigation has shown that the chironomid fauna has been severely reduced. This reduction is especially of qualitative nature, expressed by an elimination of species. As the chironomids are available to both trout and char mainly as pupae and imagines, this elimination implies that the fish after the start of regulation no longer have a constant supply of this type of food, but are restricted to a few heavy contributions that they cannot fully utilize. For instance, the enormous emergence of *Parafiefferiella batophilus* KIEFF. that occurs every year during the time 8—22 July (cf. GRIMÅS 1961, Diagr.) seems on the whole to be unutilized. Table 10 also gives the impression that a certain quantitative decrease has occurred especially in the case of char. Still more obviously, however, the elimination of species stands out (Table 11).

Table 10. The percentage of *Chironomidae* in the food of trout and char in Blåsjön.

		1944	1945	1946	1949	1954	1955	1956	1959
May—June	T	—	—	17.9	3.9	15.8	—	—	12.4
	C	—	—	3.1	37.3	53.4	—	—	7.4
July	T	26.5	—	6.1	7.5	7.0	—	4.5	5.2
	C	12.1	—	26.4	16.8	11.7	—	20.8	2.2
August	T	—	8.7	13.1	9.8	3.1	0.0	3.7	1.3
	C	—	0.2	27.9	4.8	18.4	3.0	—	0.0
September	T	—	—	5.5	14.1	0.0	—	—	6.0
	C	—	—	1.7	5.1	0.0	—	—	0.0
October	T	—	—	0.1	0.2	0.0	—	—	8.3
	C	—	—	1.5	2.9	0.0	—	—	0.0

Table 11. Number of species of chironomids found in stomachs of trout and char in Blåsjön.

	Year			
	1949	1954	1956	1959
Trout	20	11	5	6
Char	22	16	7	3

The following species of *Chironomidae* have been predominant in the food of the fish since the start of regulation:

1949

<i>Ablabesmyia</i> spp.	<i>Psectrocladius</i> sp.
<i>Macropelopia</i> sp.	<i>Cryptochironomus</i> sp.
<i>Procladius</i> sp.	<i>Parachironomus</i> sp.
<i>Heterotrissocladius Grimshawi</i> EDW.	<i>Paracladopelma obscura</i> BRUND.
<i>Heterotrissocladius subpilosus</i> KIEFF. (EDW.)	

1954

<i>Ablabesmyia</i> spp.	<i>Protanytus morio</i> ZETT.
<i>Procladius</i> sp.	<i>Psectrocladius</i> sp.
<i>Heterotrissocladius Grimshawi</i> EDW.	<i>Sergentia coracina</i> ZETT.
<i>Heterotrissocladius subpilosus</i> (KIEFF.) EDW.	<i>Tanytarsus gregarius</i> -gr.

1956

<i>Ablabesmyia</i> spp.	<i>Prodiamesa</i> sp.
<i>Procladius</i> sp.	<i>Psectrocladius fennicus</i> STORÅ
<i>Abiskomyia virgo</i> EDW.	<i>Paratanytarsus pennicillatus</i> GOETGH.

1959

<i>Procladius</i> sp.	<i>Constempellina brevicosta</i> EDW.
<i>Abiskomyia virgo</i> EDW.	<i>Tanytarsus gregarius</i> (KIEFF.) EDW.

The above list of species confirms not only the general tendency of thinning out of species, but also the change in the balance of species observed by GRIMÅS (1961), characterized, e.g., by a reduction of *Chironomini* and an increased share of *Tanytarsini* (*Constempellina brevicosta*, *Tanytarsus gregarius*) and of parthenogenetic species (*Abiskomyia virgo*).

Table 12. does not suggest any decrease in the consumption of tipulids. This substantial food is on the contrary one of the most important after regulation both as larvae and when imagines occur in masses on the water surface in connection with oviposition.

Table 12. The percentages of *Tipulidae* (larvae and imagines) in the food of trout and char in Blåsjön.

		1944	1945	1946	1949	1954	1955	1956	1959
May—June	T	—	—	2.4	1.6	1.0	—	—	14.9
	C	—	—	0.0	+	2.6	—	—	0.0
July	T	15.9	—	8.5	2.8	3.7	—	20.6	10.2
	C	13.4	—	1.3	0.0	2.6	—	11.4	1.8
August	T	—	0.6	14.8	0.8	3.7	8.7	5.8	24.3
	C	—	0.0	3.3	0.0	0.0	0.0	—	0.7
September	T	—	—	3.3	12.4	0.0	—	—	27.2
	C	—	—	1.4	0.6	0.0	—	—	0.0
October	T	—	—	0.0	0.7	0.0	—	—	1.8
	C	—	—	0.1	0.0	0.0	—	—	0.0

Tables 13 and 14 indicate that the decreased share of food originating from the bottom has been replaced by small crustaceans ("plankton") and terrestrial insects. One might ponder on the question, whether these types of food have not only gained increased importance as fish food, but also increased quantitatively in the lake. The fact that both the surface and the volume of the lake have grown during its vegetative phase permits such an hypothesis. Moreover, the decreased discharge of water during the damming-up period may result in a decreased outwash of plankton at the outlet of the lake (AXELSSON 1961). Any possible increase of this kind would, however, not form a real compensation of the loss of the more substantial bottom food.

Table 13. The percentages of small crustaceans in the food of trout and char Blåsjön. Figures within brackets apply to *Eurycercus lamellatus*.

		1944	1945	1946	1949	1954	1955	1956	1959
May—June	T	—	—	0,0	0,0	0,0	—	—	0,2 (0,2)
	C	—	—	2,4 (1,8)	1,5	27,8	—	—	16,2 (16,2)
July	T	1,8 (0,3)	—	0,0	0,4 (0,1)	2,5 (2,4)	—	0,0	0,0
	C	30,0 (5,2)	—	13,2 (10,0)	67,4	67,2 (12,5)	—	40,2 (31,0)	52,9 (7,2)
August	T	—	13,5 (8,1)	3,1 (0,6)	10,6 (10,5)	2,4	1,8	0,0	11,2 (6,1)
	C	—	83,7 (23,7)	25,3 (14,1)	87,3 (23,2)	70,1 (30,3)	56,8 (18,3)	—	92,1 (28,2)
September	T	—	—	2,9 (2,9)	3,6 (1,6)	4,3 (4,3)	—	—	41,9 (38,4)
	C	—	—	50,6 (31,5)	83,1 (5,4)	50,5 (21,2)	—	—	100,0 (44,6)
October	T	—	—	0,1 (0,1)	1,0 (1,0)	0,0	—	—	12,5 (12,5)
	C	—	—	64,2 (10,9)	82,8 (8,6)	68,4 (7,4)	—	—	96,5 (39,0)

Table 14. The percentages of terrestrial insects in the food of trout and char in Blåsjön.

		1944	1945	1946	1949	1954	1955	1956	1959
May—June	T	—	—	1.8	5.4	19.4	—	—	58.3
	C	—	—	0.0	15.4	6.9	—	—	74.2
July	T	11.9	—	6.3	13.3	46.8	—	30.0	41.9
	C	7.4	—	2.5	4.3	7.2	—	22.0	38.1
August	T	—	9.1	17.4	1.9	9.8	0.0	65.0	36.4
	C	—	0.0	3.6	0.1	0.5	13.4	—	7.2
September	T	—	—	10.7	17.7	89.3	—	—	6.0
	C	—	—	2.4	4.6	48.7	—	—	0.0
October	T	—	—	0.0	0.2	20.0	—	—	4.1
	C	—	—	2.0	< 0.1	3.4	—	—	0.0

Many types of terrestrial insects have been caught by the fish. The following list gives the dominating groups:

1946

Unidentified <i>Diptera</i>	<i>Ichneumonidae</i> (Hymenoptera)
Unidentified <i>Lepidoptera</i>	<i>Formicidae</i> (Hymenoptera)
<i>Staphylinidae</i> (Coleoptera)	<i>Apidae</i> (Hymenoptera)
<i>Elateridae</i> (Coleoptera)	<i>Jassidae</i> (Homoptera)
<i>Carabidae</i>	

1949

<i>Bibio pomonae</i> (Diptera)	<i>Ipidae</i> (Coleoptera)
<i>Fungivoridae</i> (Diptera)	<i>Carabidae</i> (Coleoptera)
<i>Phoridae</i> (Diptera)	<i>Tenthredinidae</i> (Hymenoptera)
Unidentified <i>Diptera</i>	<i>Ichneumonidae</i> (Hymenoptera)
<i>Staphylinidae</i> (Coleoptera)	<i>Cynipidae</i> (Hymenoptera)
<i>Cantharidae</i> (Coleoptera)	<i>Formicidae</i> (Hymenoptera)
<i>Elateridae</i> (Coleoptera)	Unidentified <i>Heteroptera</i>
<i>Chrysomelidae</i> (Coleoptera)	<i>Jassidae</i> (Homoptera)

1954

Unidentified <i>Diptera</i>	<i>Ichneumonidae</i> (Hymenoptera)
<i>Oporinia antumnata</i> (Lepidoptera)	<i>Formicidae</i> (Hymenoptera)
<i>Staphylinidae</i> (Coleoptera)	<i>Jassidae</i> (Homoptera)
Unidentified <i>Coleoptera</i>	<i>Psyllidae</i> (Homoptera)
<i>Tenthredinidae</i> (Hymenoptera)	<i>Aphididae</i> (Homoptera)

1956

<i>Bibio pomonae</i> (Diptera)	<i>Cantharidae</i> (Coleoptera)
Unidentified <i>Diptera</i>	<i>Scarabaeidae</i> (Coleoptera)
<i>Staphylinidae</i> (Coleoptera)	<i>Elateridae</i> (Coleoptera)

Table 15. The percentages of fish in the food of trout and char in Blåsjön.

		1944	1945	1946	1949	1954	1955	1956	1959
May—June	T	—	—	4.9	1.2	3.6	—	—	0.0
	C	—	—	0.0	2.7	0.0	—	—	0.0
July	T	1.5	—	1.7	5.2	1.6	—	0.0	9.5
	C	0.0	—	0.0	0.0	0.0	—	0.0	0.0
August	T	—	0.0	0.0	0.8	0.0	0.0	5.3	3.1
	C	—	0.0	0.0	0.0	2.0	0.0	—	0.0
September	T	—	—	1.1	0.2	0.0	—	—	0.0
	C	—	—	0.0	0.0	0.0	—	—	0.0
October	T	—	—	0.0	3.5	—	—	—	18.8
	C	—	—	0.0	0.0	0.0	—	—	0.0

*Ichneumonidae (Hymenoptera)**Jassidae (Homoptera)**Formicidae (Hymenoptera)*

1959

*Lycoridae (Diptera)**Carabidae (Coleoptera)**Fungivoridae (Diptera)*Unidentified *Coleoptera**Bibio pomonae (Diptera)**Ichneumonidae (Hymenoptera)*Unidentified *Diptera**Formicidae (Hymenoptera)*Unidentified *Lepidoptera**Bombus* sp. (*Hymenoptera*)*Staphylinidae (Coleoptera)**Tenthredinidae (Hymenoptera)**Elateridae (Coleoptera)**Psyllidae (Homoptera)*

The very considerable share of the cladocera *Eurycercus lamellatus* in the samples of 1959 could be interpreted as an effect of the restratification of sediments resulting from the increased draw down in that year.

Trout only has fed on other fish in any considerable degree. Future work may reveal, whether or not the high figures for 1949 (Table 15) imply a proceeding increase in the trout's exploitation of the char population. In this context it is of interest to note that in some Norwegian reservoirs small fractions of fast growing trout have arisen through increased predation on slow growing char (AASS 1960). In all controlled cases in Blåsjön the prey has consisted of small (probably one-year old) char. High figures in July and October may indicate that young char are then occurring within trout habitats in the litoral.

Comparison between Blåsjön and Ankarvattnet

Ankarvattnet is an unregulated lake that through its geographical situation and general character fully corresponds to Blåsjön. A comparison between the two lakes during the same time may be especially significant in the calculation of the influence of water-level fluctuations, since the heavy natural

Table 16. The food of trout in Ankarvattnet 1959 (average June—October).
Variation between size classes (total length).

	125—200	201—250	251—300	> 301
<i>Holopedium</i>	1.9	—	—	—
<i>Eurycerus</i>	5.1	3.7	—	—
<i>Gammarus</i>	53.1	51.2	43.3	100.0
<i>Limnaea</i>	0.6	2.9	—	—
<i>Trichoptera l.</i>	16.9	20.0	7.0	—
<i>Ephemeroptera l.</i>	3.2	3.0	—	—
<i>Plecoptera l.</i>	2.4	0.3	—	—
<i>Dytiscidae l.</i>	1.0	0.1	—	—
<i>Chironomidae l.</i>	0.6	0.1	—	—
<i>Trichoptera p.</i>	+	0.3	2.5	—
<i>Chironomidae p.</i>	1.1	0.2	—	—
<i>Trichoptera i.</i>	0.7	—	—	—
<i>Ephemeroptera i.</i>	3.7	—	—	—
<i>Plecoptera i.</i>	0.1	1.9	—	—
<i>Dytiscidae i.</i>	0.9	0.2	—	—
<i>Tipulidae i.</i>	7.5	11.8	16.2	—
<i>Empididae i.</i>	—	1.9	—	—
Terr. insects	1.3	2.4	31.0	—

variations between years due of climatic variations can be disregarded. The bottoms are characterized by a litoral zone grown with *Isoëtes* and with an abundance of bottom animals (cf. GRIMÅS 1961 and Fig. 3). The fishing station used in Ankarvattnet corresponding very satisfactorily to Station I in Blåsjön, the comparisons are made with the material collected at that station.

A comparison between the different size groups is given in Tables 16 and 17. The figures bear out some tendencies mentioned above concerning Blåsjön (Table 4 and 5). It is thus obvious that only the small trout have

Table 17. The food of char in Ankarvattnet 1959 (average June—October).
Variation between size classes (total length).

	125—200	201—250	251—300	> 301
<i>Bythotrephes</i>	—	1.0	1.9	1.2
<i>Bosmina</i>	30.0	8.8	0.5	—
<i>Daphnia</i>	43.3	45.9	24.3	27.3
<i>Holopedium</i>	—	3.1	—	—
<i>Eurycerus</i>	—	14.9	6.6	14.6
<i>Gammarus</i>	26.7	14.5	51.3	26.5
<i>Limnaea</i>	—	0.7	5.6	9.5
<i>Pisidium</i>	—	0.6	—	2.7
<i>Trichoptera l.</i>	—	2.6	0.5	1.9
<i>Ephemeroptera l.</i>	—	1.6	3.0	8.1
<i>Plecoptera l.</i>	—	1.2	1.2	2.2
<i>Dytiscidae l.</i>	—	—	—	1.2
<i>Chironomidae l.</i>	—	—	—	2.1
<i>Trichoptera p.</i>	—	4.8	5.0	—
<i>Chironomidae p.</i>	—	0.2	0.2	2.7

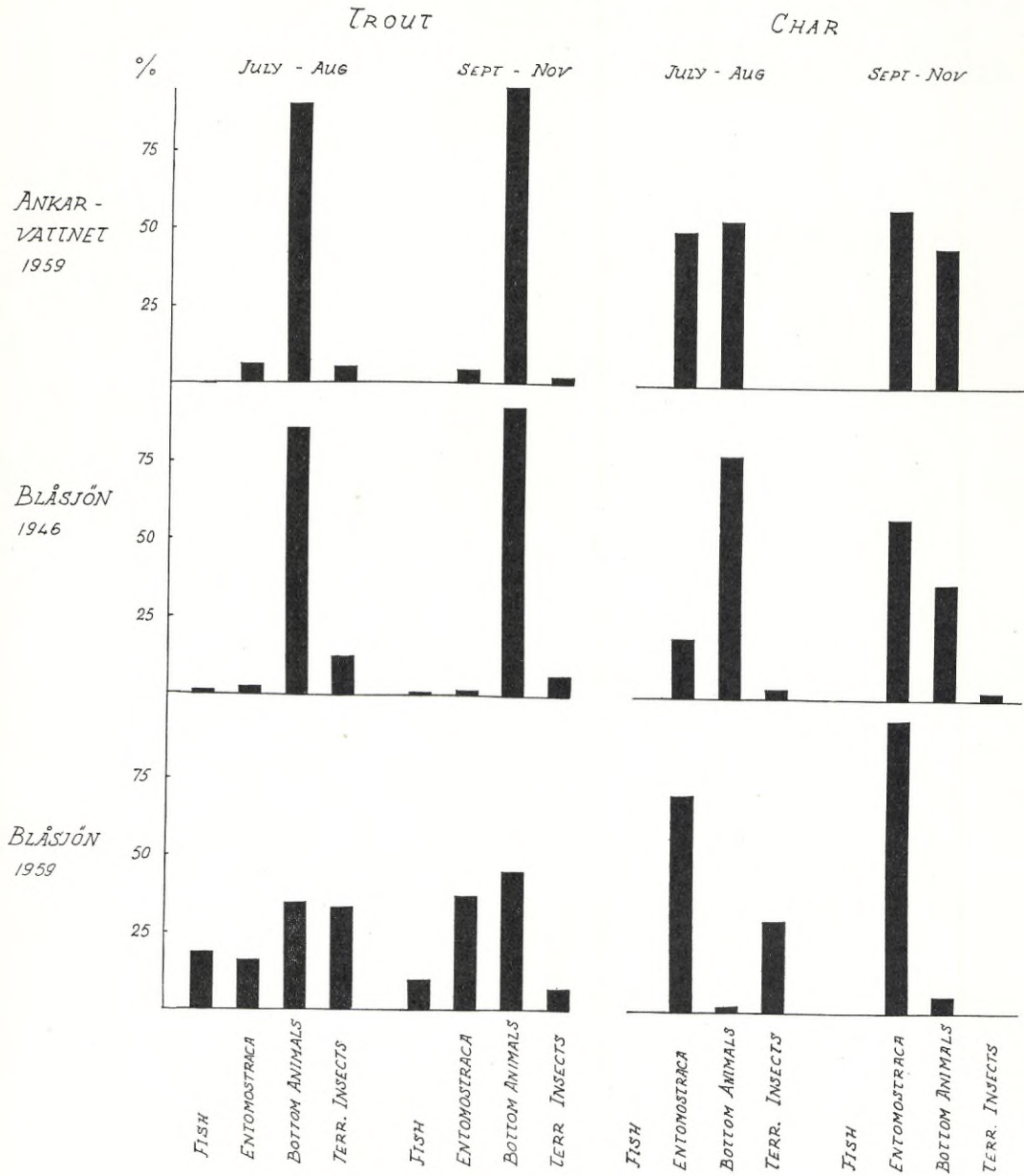


Fig. 4. Comparison between the food of trout and char in Ankarvattnet (1959) and Blåsjön before the start of regulation (1946) and ten years after the start of regulation (1956).

Table 18. Comparison between the feeding habits of trout and char in Blåsjön (Station I) and Ankarvattnet 1959.

	Trout				Char			
	July—Aug.		Sept.—Nov.		July—Aug.		Sept.—Nov.	
	Blå-sjön	Ankar-vattnet	Blå-sjön	Ankar-vattnet	Blå-sjön	Ankar-vattnet	Blå-sjön	Ankar-vattnet
Fish	18.2	—	9.1	—	—	—	—	—
<i>Bythotrephes</i>	—	—	—	—	—	4.0	1.3	—
<i>Bosmina</i>	—	—	—	—	3.7	—	—	7.9
<i>Daphnia</i>	—	—	—	—	5.9	40.0	43.4	29.2
<i>Holopedium</i>	—	1.5	—	—	0.8	—	—	2.0
<i>Eurycercus</i>	15.4	4.3	35.9	3.8	52.9	4.4	50.5	16.8
<i>Heterocope</i>	—	—	—	—	5.9	—	—	—
<i>Gammarus</i>	—	61.3	—	38.5	—	36.4	—	36.8
<i>Limnaea</i>	—	1.4	5.0	1.8	—	5.1	—	5.1
<i>Trichoptera l. (Apatania)</i>	—	3.5	—	33.9	—	—	—	2.1
<i>Ephemeroptera l.</i>	15.8	4.8	—	—	—	0.9	—	—
<i>Plecoptera l.</i>	4.6	—	31.8	3.2	—	—	4.8	0.1
<i>Dytiscidae l.</i>	—	0.9	0.6	—	—	—	—	—
<i>Chironomidae l.</i>	—	0.1	9.1	0.7	—	—	—	—
<i>Tipulidae l.</i>	3.6	—	—	—	—	—	—	—
<i>Trichoptera p.</i>	0.9	3.6	—	—	—	8.9	—	—
<i>Chironomidae p.</i>	9.1	1.1	0.3	—	1.4	0.3	—	—
<i>Trichoptera i.</i>	—	0.2	—	0.6	—	—	—	—
<i>Plecoptera i.</i>	—	0.1	—	2.1	—	—	—	—
<i>Dytiscidae i.</i>	—	0.1	—	1.1	—	—	—	—
<i>Tipulidae i.</i>	—	8.0	2.3	12.6	—	—	—	—
<i>Empididae i.</i>	—	4.4	—	0.2	—	—	—	—
Terr. insects	32.4	4.7	5.9	1.4	29.4	—	—	—

eaten *Eurycercus*, while surface food (*Tipulidae* and terrestrial insects) have been consumed mainly by big fish. As in Blåsjön the small char have been feeding mainly on small crustaceans (*Bosmina*, *Daphnia*), while bottom animals such as *Limnaea* and ephemerid larvae have been eaten mostly by big fish.

Many of the tendencies deduced from the examination of the variation between different years in Blåsjön are confirmed by the comparison with Ankarvattnet (Table 18 and Fig. 4). The more obvious tendencies are summarized as follows:

1. Fish (young char) are important food of trout in the regulated lake.
2. *Eurycercus lamellatus* is more frequent in the regulated lake as food of both trout and char.
3. *Gammarus lacustris* is a very important food of both trout and char in the unregulated lake, but entirely lacking in the regulated lake.
4. *Limnaea* is more frequent as food in the unregulated lake.
5. *Trichoptera* in the form of larvae, pupae, and imagines (*Apatania* sp.) are more frequent as food in the unregulated lake.

6. There is no obvious difference in the consumption of *Ephemeroptera*, although one species only (*Siphonurus lacustris*) is found in Blåsjön, while Ankarvattnet contains four species (*Siphonurus lacustris*, *Ameletus inopinatus*, *Leptophlebia vespertina* and *Heptagenia fuscogrisea*).

7. *Plecoptera* larvae (mainly *Nemoura avicularis*) are more frequent as food in the regulated lake.

8. Terrestrial insects are more frequent as food in the regulated lake.

6. The feeding habits of the fish in Jormsjön after water-level regulation

Table 19 shows the dietary state of the fish in Jormsjön after regulation.

It is obvious that the feeding habits of the fish in Jormsjön have not been affected at all by water-level fluctuations in the same degree as in Blåsjön. For instance, the important prey species *Gammarus lacustris* and *Asellus aquaticus* occur to a remarkable extent as food both of trout and char.

The changes that can be discerned within the present material are a tendency in both species towards an increased consumption of terrestrial insects and a tendency in trout towards increased consumption of fish. Both tendencies are in agreement with what has happened in Blåsjön.

The relatively small influence may result from the circumstance that the water-level fluctuations are not sufficiently great for the complete elimination of any prey species and also from the preserving effect of the impounded area at "Libotten".

7. Conclusions

In the previous chapters has been established that the changes in the abundance and composition of the prey fauna occurring as results of artificial water-level fluctuations act essentially upon the feeding habits of the fish. Some important prey species (e.g. *Gammarus*) disappear or get rare, others (e.g. terrestrial insects) increase in importance.

The decrease in growth rate occurring some years after the start of water-level regulation that has been established from many other lakes (cf. e.g. RUNNSTRÖM 1951) could be explained only upon the basis of this change from a substantial, constantly available food to a less substantial, more occasional food, but also the "over-production" of nourishment occurring during the first years of damming-up might contribute to a decreased growth rate because of rich year classes and a resulting stunting (RUNNSTRÖM 1951).

The present material confirms at all events that the process that has been started will develop slowly: there is no reason to believe that there a new

Table 19. The food of trout and char in Jormsjön after the start of regulation.

	Trout			Char		
	June—July 1955	Sept. 1955	June—July 1956	June—July 1955	Sept. 1955	June—July 1956
Fish	9.8	4.0	4.6	—	2.0	—
<i>Phyllopoda</i> , indet.	—	—	—	2.0	4.1	—
<i>Bythotrephes</i>	—	0.4	—	—	0.8	—
<i>Bosmina</i>	—	—	—	—	—	14.8
<i>Daphnia</i>	—	—	—	—	6.1	1.9
<i>Holopedium</i>	—	—	—	—	18.2	—
<i>Eurycercus</i>	—	—	—	—	7.2	—
<i>Heterocope</i>	—	—	—	—	10.9	—
<i>Gammarus</i>	9.7	12.7	5.7	18.7	2.3	3.6
<i>Asellus</i>	24.3	10.9	23.5	20.8	28.0	18.2
<i>Limnaea</i>	6.2	7.0	1.1	0.2	—	7.9
<i>Planorbis</i>	4.2	0.8	2.0	—	—	—
<i>Pisidium</i>	—	—	—	0.3	1.0	—
<i>Bryozoa</i> , statoblasts ..	—	0.8	—	—	—	—
<i>Oligochaeta</i>	—	—	4.0	—	—	—
<i>Trichoptera l.</i>	18.2	18.8	8.7	0.6	—	3.9
<i>Ephemeroptera l.</i>	1.4	0.4	4.4	8.9	—	0.2
<i>Plecoptera l.</i>	2.7	—	3.8	0.5	0.6	1.9
<i>Sialis l.</i>	—	—	0.3	—	—	0.4
<i>Dytiscidae l.</i>	0.2	—	—	0.3	—	—
<i>Chironomidae l.</i>	0.1	0.2	0.3	6.6	—	3.8
<i>Ceratopogonidae l.</i> ...	—	—	—	—	—	0.4
<i>Simuliidae l.</i>	—	—	—	0.4	—	2.9
<i>Tipulidae l.</i>	1.2	—	—	—	—	0.1
<i>Diptera l.</i>	—	—	—	—	—	1.7
<i>Trichoptera p.</i>	—	—	—	—	1.0	—
<i>Chironomidae p.</i>	—	0.2	6.8	23.1	—	7.1
<i>Ephemeroptera i.</i>	—	0.1	—	—	—	—
<i>Plecoptera i.</i>	0.5	—	—	—	—	0.1
<i>Sialis i.</i>	—	—	—	—	—	1.1
<i>Dytiscidae i.</i>	3.5	0.1	1.0	1.1	—	0.6
<i>Chironomidae i.</i>	1.0	3.0	—	1.8	0.7	1.1
<i>Tipulidae i.</i>	—	0.4	2.0	1.2	3.8	1.7
Terr. insects	15.8	38.6	31.0	13.5	13.0	26.6
Plants	1.2	—	0.8	—	0.3	—
Inorganic comp.	—	1.4	—	—	—	—

equilibrium in the organic life should have been established even ten or twenty years after the start of regulation. In the case of Blåsjön it is not probable that any essential changes in the growth rate of the char should have occurred yet, especially as many of the summers following upon the start of regulation have been thermically beneficial to the growth of the fish. A significant difference in quality between the trout of Blåsjön and the trout of Ankarvattnet, the Blåsjön-trout being thinner, may indicate that the weight has been affected (Fig. 5).

It could be expected that trout should be the most severely suffering species as it is bound to the litoral zone of the lake during the important part of the growth period, without being able to leave it though the significant prey species have disappeared or have been essentially thinned out (cf. Fig. 6).

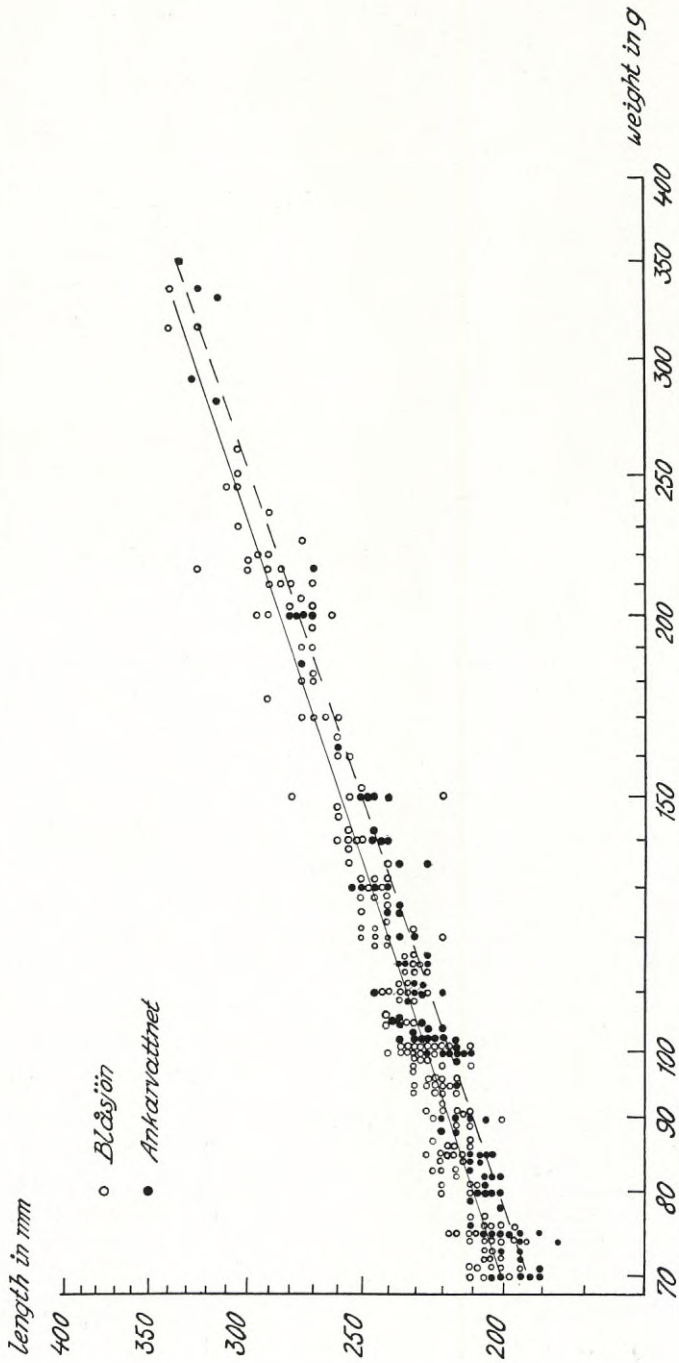


Fig. 5. Length — weight relationship of trout from Blåsjön and Ankarvattnet.

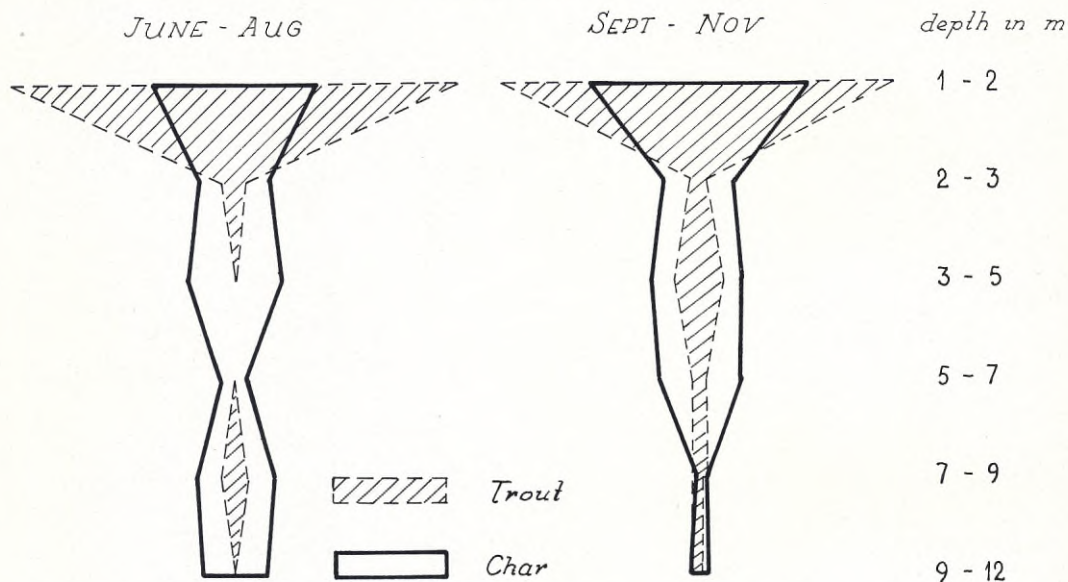


Fig. 6. Vertical distribution of the catch of trout and char in Blåsjön (per cent of total catch).

Char, on the other hand, feeds already in natural condition in an essential degree on plankton, though it lives on more substantial food during the growth period in spring and early summer. There are thus reasons to believe that the changes in growth rate caused by changed feeding habits should be less drastic in the case of char than in the case of trout which on account of its ecological "rigidity" is forced to search after the small remnants of littoral food. To this difference may be added also the difference in behaviour between the two species involving a tendency towards territorial behaviour in trout and a more roaming behaviour in char that permits feeding, where opportunity avails itself. The mouths of the inlet rivers and brooks and impounded areas like "Libotten" in Jormsjön are very important as food refuges for the fish after the artificial water-level fluctuations have started.

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