FISHERY BOARD OF SWEDEN

INSTITUTE OF FRESHWATER RESEARCH

DROTTNINGHOLM

Report No 39

LUND 1958
CARL BLOMS BOKTRYCKERI A.-B.

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Table of Contents

Ein planktologisches Querprofil

Von BRUNO BERZINS, Aneboda
Södra Sveriges Fiskeriförening

Die Diskussion über Wolken- und Schwarmbildung des Zooplanktons in Seen (TONOLLI, ELSTER) auf dem dreizenten Limnologenkongress veranlasst mich, eine frühere Untersuchungsserie zu veröffentlichen, um meinerseits mit einem kleinen Beitrag zur Lösung diese Fragen beizutragen. Über die obengenannten Wolken- und Schwarmbildungen des Zooplanktons habe ich bisher in der vorliegenden Literatur noch keinen guten illustrativen Querschnitt gesehen. Deshalb habe ich eine Anzahl von Diagrammen angefertigt, um einen besseren Einblick in die Verteilungsverhältnisse der verschiedenen Arten und Gruppen zu bekommen.

Es gibt eine Reihe von Arbeiten über vertikale Planktonprofile, aber hier sind die Abstände zwischen den Beobachtungspunkten viel zu gross, nicht nur Hunderte sondern sogar Tausende von Meter. Es wurde daher kein gutes Gesamtbild erreicht. Diese Verhältnisse gaben mir Anlass, den Versuch zu machen, die Planktonverteilung sowohl vertikal als auch horizontal aber auf einen engeren Raum begrenzt, zu studieren. Als Studienobjekt wurde den 36 ha grosse Skärshult-See (Südschweden, Aneboda Gebiet) gewählt, welcher schon früher von mehreren Limnologen untersucht worden ist (LÖNNERBLAD 1931, GESSNER 1934, THUNMARK 1942, ÅBERG & RODHE 1942, BRUNDIN 1949, etc.).

Methodik

In den eingesammelten Proben wurde nur Zooplankton analysiert, weil für das Gesamtplankton die Zeit nicht ausgereicht hätte und auch werden eine etwas abweichende Arbeitsmethodik angewandt sollte.

Ausser Planktonproben wurden auch einige Wasserproben untersucht, um einen Überblick über einige Milieufaktoren zu erhalten.

Die Temperaturverhältnisse wurden bei allen Proben kontrolliert, dagegen wurde Sauerstoff nur in einigen Vertikalserien analysiert. Die Wasserfarbe (Pt), pH, Eisen und organische Stoffe wurden nur in den Proben der tiefsten Stationen untersucht.

Am Nordende des Skärshult-See, gegenüber von Gabrielsberg wurde das planktologische Querprofil gelegt. An dieser Stelle geht der Uferfelsen ohne Haldenbildung bis zu einer Tiefe von 12 m hinab, um dann nach weiteren 30 m westlich die grösste Tiefe des Sees zu erreichen (14 m). Das Westufer

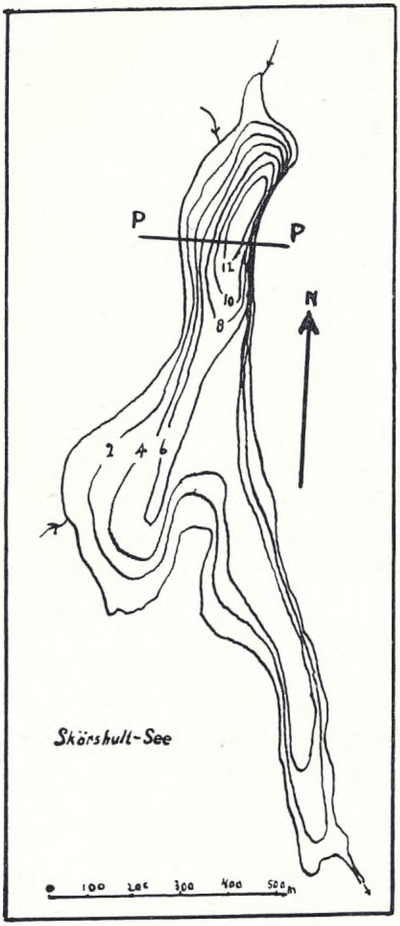

Abb. 1. Tiefenkarte über den Skärshult-See (nach Gessner). PP=planktologisches Querprofil.

dagegen besteht aus Moränenkies, welcher über die wohlgebildete Halde in die Tiefe geht. Das Ostufer beim Gabrielsberg war vegetationsfrei, dagegen hatte sich am westlichen Ufer eine ziemlich breite Pflanzenzone gebildet. Von Schwimmpflanzen waren da *Nuphar* und *Potamogeton natans,* von Helophyten einzelne *Phragmites* vertreten. Dagegen war *Equisetum limosum* reichlicher in der Ufernähe angesammelt. Von Elodeiden wurden nur einige *Myriophyllum alterniflorum* in der Profillinie gesichtet. Dagegen bildeten die Elodeiden zusammen mit den Isoetiden einen ziemlich dichten Pflanzenbestand ganz am Ufer: *Lobelia Dortmanni* und *Juncus bulbosus.*

Der See ist hier nur 145 m breit. Vom Gabrielberg nach dem Westufer wurde in die Wasserlinie eine Leine gespannt, an der dann die Stationen mit einem schwimmenden Korken gekennzeichnet wurden. Das Boot wurde am Korken angebunden und die Proben von dem festgebundenen Bootsende aus dem See entnommen. So konnte eine Pendelbewegung des Bootes fast vollständig eliminert werden. Die Proben wurden so schnell wie möglich entnommen, um Zeit zu gewinnen und dadurch gange Material mehr einheitlich zu erhalten. Die Verkürzung der Einsammlungszeit war eine Massnahme, die im wesentlichen eine eventuelle Wanderung der Planktonorganismen ausschliesst. Ebenso war ein Zeitpunkt gewählt worden, bei welchem das geringste Wanderungsphenomen zu erwarten war, nämlich kurz nach der Mittagszeit, weil dann die Wanderung nach der Tiefe zu abgeschlossen ist und die Abendwanderung nach oben noch nicht angefangen hat. Trotz dieser Eile dauerte es eine Stunde und 50 Minuten, um das ganze Profil durchzugehen, nämlich von 14.00—15.50.

An diesem Tag, dem 7 August 1950, schien während des ganzen Tages die Sonne bei wolkenlosem Himmel. Nur wehte ein ziemlich scharfer Wind (NO-Wind) vom Gabrielsberg her, aber der relativ hohe Wald schwächte den Wind ab.

Noch immer fehlt es an einer einwandfreien, quantitativen Planktonuntersuchungstechnik, wie es sich bei der Diskussion während des vorigen Limnologenkongresses in Finnland zeigte. Selbst habe ich früher eine Reihe von Versuchen gemacht, um eine besserte Methodik auszuarbeiten. Auch mit dem RHODEs Wasserschöpfer (5 L) habe ich Proben genommen und herausgefunden, dass dieser für meine Profiluntersuchungen sehr gut ausreicht. Hierbei wird ein offener Zylinder hinab gelassen, der beim Zuschliessen dann ein Wasservolumen mit allen Tieren enthält, die sonst oft durch Leinen, Klappen oder Bugwellen mindestens teilweise verscheucht wurden, d.h. auch die beweglicheren Formen wurden nahezu alle mit erfasst. Das geht nicht mit den meisten Apparaten, die sonst in Frage kommen, sodass ich den RHODEs Schöpfer benutzt habe.

Man könnte einwenden, dass es wünschenswert wäre, einen Apparat von 10 L Grösse zu benutzen, oder sogar zweimal fünf Liter zu schöpfen. Aber meine früheren Versuche überzeugten mich, dass für die geplante Profiluntersuchung ein 5 L Schöpfer ausreichte. Ein mehrmaliges Aufholen des Wasserschöpfers hilft wegen Zeitverlust und Wasserwirbeln beim Auf- und Ablassen etc. auch nicht viel. Die Diagramme wären dadurch kaum klarer geworden.

Weil Nannoplankton und überhaupt Phytoplankton nicht berücksichtigt worden sind, wurden die Proben durch ein Planktonnetz aus Seidengaze Nr. 25 filtriert und mit Formalin fixiert. Später wurden alle Zookomponenten in den Proben, ebenfalls mit Hilfe einer Zentrifuge, total gezählt und ich begnügte mich nicht allein mit Stichprobenanalysen. Dadurch konnten hier Fehlerquellen vermieden werden.

Zugleich wurden damit auch alle *Kellicottia longispina* gemessen. Beim Anfertigen von Diagrammen wurde von logarithmischen Werten abgesehen, weil auf der Fläche für Isolinien die absoluten Zahlen sehr gut gebraucht werden konnten.

Die physikalisch-chemischen Eigenschaften wurden mit den sonst in der Limnologie üblichen Analysierungsmethoden bestimmt.

Die chemisch-physikalischen Eigenschaften

Am 7. August 1950 hatte sich im Skärshult-See eine sehr stabile Schichtung gebildet. Das Epilimnion war bei einer Wassertemperatur von 17—20°C ca. 4 m dick. Mit einem Temperaturfall von 8° war das Metalimnion höchstens 3 m dick. Unter der 6—7 m Linie hatte sich das Hypolimnion bei ung. 9°C verlagert.

Sauerstoff war noch genügend im oberen Teil des Metalimnions vorhanden, aber dann verminderte er sich stark, und in dem Hypolimnion war nur etwas Sauerstoff übrig. Jedoch kam ein totaler Sauerstoffschwund am Boden nicht vor.

Tabell I. Temperatur und Sauerstoff in Skärshult-See am 7/VIII 1950.

m	Station III			Station V			Station VII		
	t°	O_2 mgl	%	t°	O_2 mgl	%	t°	O_2 mgl	%
0	19,2	8,33	87,4	19,1	8,36	87,8	19,0	8,30	86,8
2	19,0	8,83	92,4	19,0	9,11	95,3	—	—	—
3	19,0	8,29	86,8	—	—	—	19,0	8,92	93,3
4	16,8	7,38	74,0	16,7	7,32	73,3			
5	14,3	6,98	66,6	—	—	—			
6	12,3	2,19	20,0	11,1	2,16	19,3			
7	10,1	1,47	12,2	—	—	—			
8	9,5	1,06	9,1	9,2	1,11	9,5			
10	8,4	0,29	2,4						
12	8,1	0,07	0,6						

Die Wasserreaktion war sauer, doch nicht unter pH 6,3. Bei 3 m Tiefe war pH etwas höher, wahrscheinlich infolge der Assimilationstätigheit des Algenplanktons.

Der stark mesohumose See mit einer Wasserfarbe von 45 Pt mgl an der Oberfläche war am Boden fast 4 mal dunkler, nämlich 165 Pt mgl. Parallel hierzu verlief die Verteilung von Eisen: von 0,3 tot. Fe mgl an der Oberfläche, 1,1 mgl bei 9 m Tiefe und 2,4 mgl in die Bodennähe. Die Oxydation durch Kaliumpermanganat war bis zu 9 m wenig veränderlich (57—70 mgl $KMnO_4$-Verbr.) und stieg in der Tiefe etwas an (bei 12 m auf 114 mgl). Das dunkle, humusreiche Wasser schützte auch bei vollem Sonnenschein die Planktontiere mehr vor starken Belichtung, als das bei Klarwasserseen möglich wäre.

Bei näherer Betrachtung der Sprungschicht sieht man, dass der obere Teil am Gabrielsberg nach oben gehoben und an der Westseite etwas nach unten gedrückt worden ist. In der Mitte jedoch ist die Thermokline dünner geworden. Das kalte Tiefenwasser hat diese nach oben gepresst.

Die Verschiebung des Metalimnion ist sicher von dem starken NO-Wind verursacht worden, welcher den ganzen Vormittag über dem Gabrielsberg wehte und die oberen Wasserschichten von der Seemitte aus gegen das zentrale Seebecken im Süden drückte. Der verminderte Druck im nördlichen Teil des Sees wurde von der Seite her kompensiert. Ausserdem kam von dem

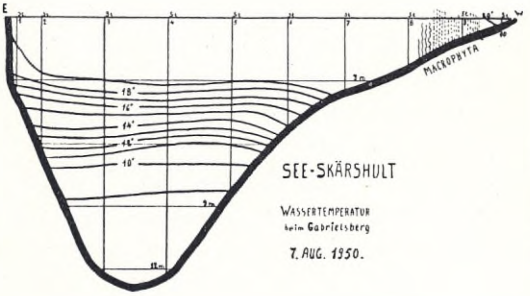

Abb. 2. Wassertemperatur in Skärshult-See am Gabrielsberget den 7/8 1958. Die Beobachtungsstationen und ebenso die Pflanzenzone sind eingetragen.

Tabell II. Skärshult-See, Station III. Einige Milieufaktoren am 7/VIII 1950.

m	Farbe Pt mgl	pH	Ges. Fe mgl	$KMnO_4$—Verbr. mgl
0	45	6,6	0,3	56
3	60	6,7	0,3	58
6	120	6,4	0,6	68
9	140	6,3	1,1	70
12	165	6,3	2,4	114

zentralen Becken des Sees eine Tiefenströmung mit kälterem Wasser als Substitut für das fortgedrängte Wasservolumen zurück. Da der Wind schief gegen die Längsachse des Sees wehte, und einen stärkeren Druck auf der westlichen Seeseite ausübte, wurde die Sprungschicht schräg verschoben. Diese Wasserzirkulation hat auch teilweise die Planktonverteilung beeinflusst, was bei Betrachtung der Verteilungsbilder berücksichtigt werden muss.

Das Querprofil

Zuerst wird ein Verzeichnis der im Plankton gefundenen Arten gegeben, wobei auch die Menge der Individuen per 1 m^3 gezeigt wird. Diese Zahl ist als Mittelwert für das ganze Querprofil errechnet worden. Eine nähere Analyse der Ergebnisse wird in der folgenden Darstellung und ebenfalls in den beigefügten Diagrammen gegeben.

Tabelle III. Die im Profil gefundenen Arten, und der Mittelwert für 1 cbm Wasser im Querprofil.

Rotatoria	
Ascomorpha ecaudis (Perty)	43
Ascomorpha ovalis (Bergendal)	530
Ascomorpha saltans Bartsch	11
Asplanchna herricki de Guerne	510
Asplanchna priodonta Gosse	1.480
Collotheca libera (Zacharias)	420
Collotheca mutabilis (Hudson)	4.620
Collotheca pelagica (Rousselet)	16.280
Colurella b. bicuspidata (Ehrenberg)	2
Colurella denticauda Carlin	2
Conochilus hippocrepis (Schrank)	60
Conochilus unicornis Rousselet	1.230
Euchlanis d. dilatata Ehrenberg	5
Euchlanis meneta Myers	5
Filinia longiseta (Ehrenberg)	140
Gastropus sylifer Imhof	660
Kellicottia longispina (Kellicott)	45.680
Keratella c. cochlearis (Gosse)	25.780
Keratella cochl. hispida (Lauterborn)	1.080
Keratella hiemalis Carlin	20
Lecane elasma Harring & Myers	5

Lecane intrasinuata (Olofsson)	4
Lecane l. lunaris (Ehrenberg)	10
Lecane scutata Harring & Myers	3
Lecane stenroosi (Meissner)	5
Lepadella patella (Muller)	140
Monommata sp.	2
Ploesoma hudsoni (Imhof)	130
Polyarthra euryptera Wierzejski	4.280
Polyarthra longiremis Carlin	1.100
Polyarthra major Burckhardt	2.350
Polyarthra remata Skorikov	1.720
Polyarthra vulgaris Carlin	8.430
Synchaeta oblonga Ehrenberg	480
Testudinella p. parva (Ternetz)	3
Testudinella vidzemensis Berzins	5
Trichocerca capucina (Wierzejski & Zacharias)	290
Trichocerca longiseta (Schrank)	2
Trichocerca myersi (Hauer)	16
Trichocerca rousseleti (Voigt)	610
Trichocerca similis (Wierzejski)	890

Ausserdem einige unbestimmbare *Bdelloidea* und *Illoricata.*

Copepoda

Cyclops str. strenuus (Fischer)	108
Eudiaptomus gracilis (Sars)	4.680
Mesocyclops oithonoides (Sars)	1.180
Mesocyclops leuckarti (Claus)	52
Heterocope appendiculata Sars, inkl. copepoditer	42
Nauplier, hauptsächlich Cyclopider	12.150
Copepoditer	9.330

Cladocera

Alonopsis elongata Sars	9
Bosmina coregoni longispina Leydig	1.230
Bosmina longirostris similis Lilljeborg	860
Ceriodaphnia q. quadrangula (Muller)	390
Daphnia cristata cederströmi (Schoedler)	2.550
Diaphanosoma brachyurum (Lieven)	3.380
Eurycercus lamellatus (Muller)	4
Holopedium gibberum Zaddach	30
Leptodora kindti Focke	14
Limnosida frontosa Sars	200
Polyphemus pediculus (Linné)	1.020

Bei den Copepoden war die dominierende Art *Eudiaptomus gracilis,* subdominant gefolgt von *Mesocyclops oithonoides.* Bei den Cladoceren war *Diaphanosoma brachyurum* reichlich vertreten, gefolgt von *Daphnia cristata cederströmi* und ferner von *Bosmina coregoni longispina,* sowie im Litoral von *Polyphemus pediculus.* Die dominierende Art unter den Rotatorien war *Kellicottia longispina,* subdominant *Keratella c. cochlearis,* gefolgt von *Collotheca pelagica, Polyarthra vulgaris, Coolotheca mutabilis* und *Polyarthra euryptera.*

Die Crustaceen

Die planktischen ad. *Copepoda* und *Cladocera* (Abb. 6) haben die westliche Seite der östlichen vorgezogen, weil sich hier in der Nähe der Vegetation die höchste Konzentration befand. In der Bodenschicht ausserhalb der Vegeta-

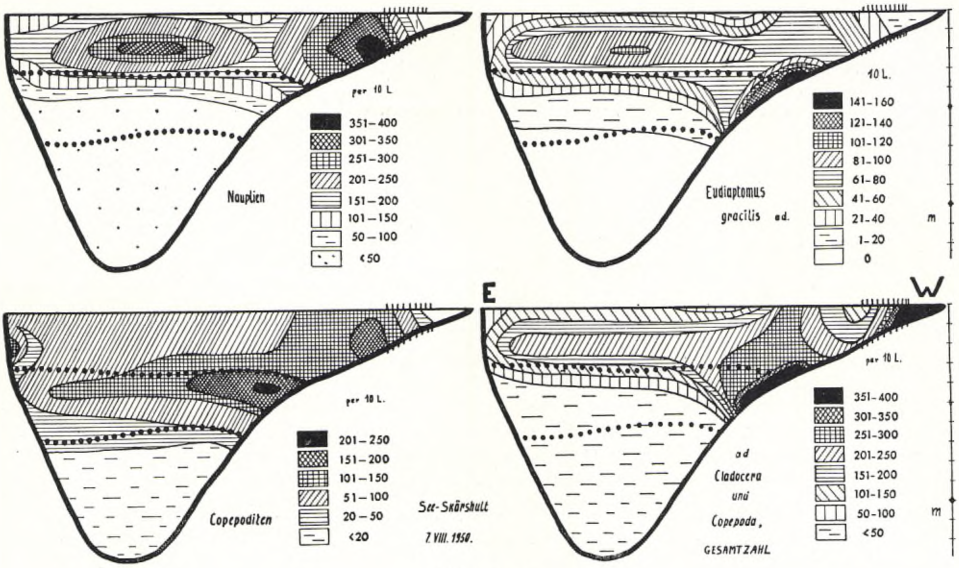

Abb. 3—6.

tionszone liegt die Anhäufung von vollerwachsenen Tieren im unteren Epilimnion ebenso wie im oberen Metalimnion. Von hier aus, strahlten die Tiere im Epilimnion zum östlichen Ufer hinaus. Im Hypolimnion und unteren Teil des Metalimnions sind diese adulten Tiere weniger vertreten. Ein hohes Maximum liegt auch auf der Landseite am westlichen Ufer, wo hinter den Gewächsen eine starke Konzentration von nur einer Art vorherrscht: *Polyphemus pediculus.* Das Gesamtbild zeigt, dass man hier von einer Schwarmbildung sprechen kann, weil die Tiere hier durch aktive Wanderung angehäuft sind. Flucht vor starker Beleuchtung, Ausweichen vor einem niedrigen Sauerstoffdruck, eventuellt auch Flucht vor niedrigen Temperaturen, haben die Tiere gegen das westliche Ufer geführt, weil dort die Beschattung durch Pflanzen wie auch schwimmende Detrituspartikel (die in den Planktonproben reichlich vorkamen) in der bodennahen Schicht für die negativ phototaktische Tiere mehr optimale Verhältnisse schaffte. Die Copepoditen haben ein ähnliches Verteilungsbild ergeben, doch gehen diese Stadien tiefer ins Metalimnion hinein. Ebenso kann eine stärkere Ansammlung in der Zone der Nymphaeiden beobachtet werden. Dass diese Tiere mehr von den Strömungen beeinflusst werden, zeigt ein nach oben gerichtetes Bestreben am östlichen Ufer, wo ein Teil der Copepoditen (Abb. 5) mehr oder weniger passiv mitfolgt. Was die Nauplien (Abb. 3) anbetrifft, so liegt die grösste Anhäufung in der Zone der Gewächse, wobei auch eine schwächere Anhäufung im Zentrum des Epilimnions vorkommt.

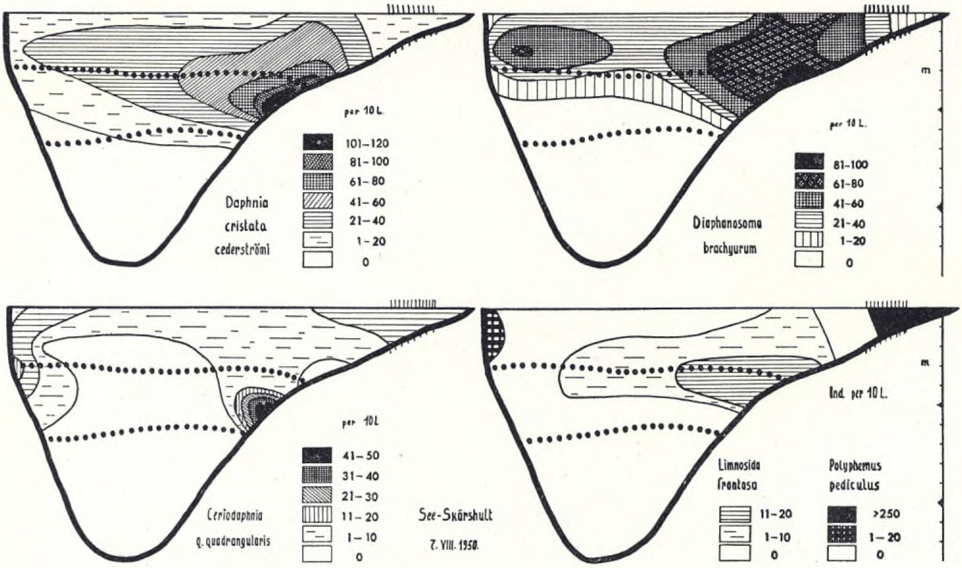

Abb. 7—10.

Die Arten

Eudiaptomus gracilis (SARS) (Abb. 4). Die grösste Anhäufung dieser Art befindet sich in den bodennahem Schicht der Station 7, mit einem Maximum von 150 Tiere pro 10 L. Von hier strahlt eine kleinere Anzahl Tiere ins Epilimnion aus. Einzelne kommen im Metalimnion vor, aber keine im Hypolimnion. Nur einzelne gehen in die Zone der Elodeiden hinein. Eine aktive Schwarmbildung liegt vor.

Mesocyclops oithonoides (SARS) (Abb. 16). Diese Art hatte die grösste Anhäufung mit 52 Ind./ 10 L in 2 m Tiefe bei Station 8, also in der Zone der Schwimmpflanzen. Sonst ist sie sparsam im Epilimnion, etwas im Metalimnion, aber nicht im Hypolimnion vertreten.

Mesocyclops leuckarti (CLAUS). Nur vereinzelte Tiere im Profil.

Cyclops s. strenuus (FISCHER) (Abb. 16). Nur im Hypolimnion vertreten, wo ein Maximum von 13 Ex./ 10 L vorkam, sind aber sonst nur sparsam verteilt. Diese Art hat das 8—9° kalte Tiefenwasser mit einem Sauerstoffgehalt von höchstens 12 % Sättigung bevorzugt, also, eine kaltstenotherme Art, welche eine sehr niedrige Sauerstoffmenge überleben kann (z.B. 0,07 mgl), wenn sie auch in der Zeit der Hochproduktion (Frühjahr) dieser Art im sauerstoffreichen Milieu lebt.

Heterocope appendiculata SARS. Nur einige erwachsene Tiere und einige Copepoditen wurden angetroffen.

Diaphanosoma brachyurum (LIEVEN) (Abb. 8). Interessant ist, dass auch diese planktische Cladocere ihre grösste Anhäufung in der bodennahen

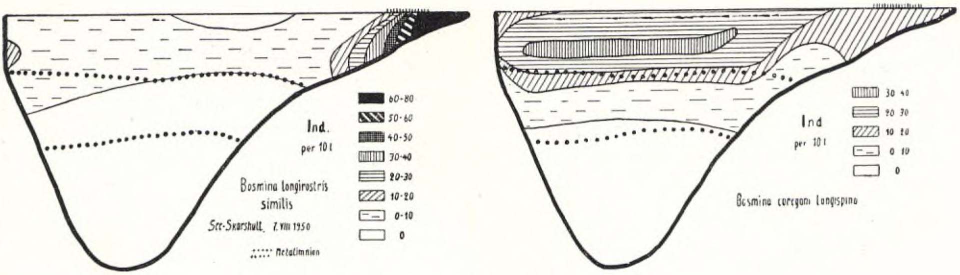

Abb. 11—12.

Schicht vor den Schwimmpflanzen hatte, wobei auch der obere Teil des Metalimnion berührt wurde. Eine kleinere Konzentration kommt auch am östlichen Ufer über der Sprungschicht vor. Doch geht kein Tier ins Hypolimnion hinein.

Daphnia cristata cederströmi (SCHROEDLER) (Abb. 7). Sie hat ein ähnliches Verteilungsbild wie Diaphanosoma, wenn auch das Maximum etwas tiefer liegt. Es gingen auch mehr Tiere in die Sprungschicht hinein.

Ceriodaphnia q. quadrangula (MULLER) (Abb. 9). Sie war nicht reichlich vertreten. Maximum 43 St./ 10 L (Stat. 6, 5 m) war an der westlichen Seite des Sees gelegen.

Limnosida frontosa SARS (Abb. 10). Sie war pelagisch im unteren Epilimnion und im oberen Metalimnion vertreten und wurde nur im westlichen Teil des Sees angetroffen.

Holopedium gibberum ZADDACH. Es wurden nur einige Individuen an der Station 7 gefunden.

Polyphemus pediculus (LINNÉ). Diese Art kam nur ganz nahe am Ufer vor, besonders reichlich am westlichen Seeseite, wo sich eine Anhäufung von 264 fand.

Leptodora kindti FOCKE. Es wurden nur einige Tiere an der Stat. 7 in 2 m Tiefe gefunden.

Bosmina coregoni longispina LEYDIG (Abb. 2). Diese Cladocere war ziemlich gleichmässig in dem mittleren Teil der Epilimnion und sparsam im Metalimnion verteilt. Markant ist, das diese Art keine Anhäufung am westlichen Ufer hat, was bei Crustaceen durchweg der Fall ist.

Bosmina longirostris similis LILLJEBORG (Abb. 11). Die Schwarmbildung dieser Art unterscheidet sich wesentlich von derjenigen der *longispina,* weil die Verteilung auf die westliche Seeseite in und hinter der Zone der Pflanzen beschränkt ist.

Rotatoria

Diese Tiere haben ein schwächeres Vermögen der Wasserströmung entgegenzuarbeiten. Sie werden vielmehr von Turbulenzströmungen transportiert, und bilden somit mehr „Planktonwolken“. Jedoch ist es nicht so leicht,

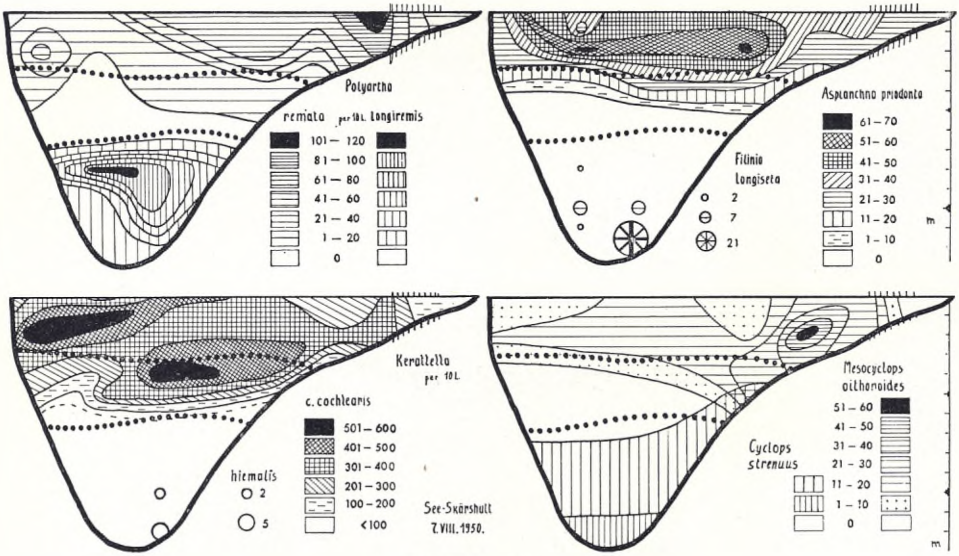

Abb. 13—16.

ganz einfach alle Rädertiere unter dieser Benennung unterzubringen. Wenn man auf die Verteilungsverhältnisse bei *Polyarthra major, Trichocerca similis* (event. auch anderer Arten) sieht, dann finden wir, wie stetig sie sich in einem begrenzten Gebiet halten, und dass nur wenige von Strömungen mitgenommen werden. Es scheint somit, dass die von Elster vorgeschlagenen Benennungen „Schwärme“ und „Wolken“ keine festen Abgrenzungen haben. Nicht nur an den Rotatorien können wir solche Beobachtungen machen, sondern ebenso verhalten sich auch Copepoditen u.a.

Kellicottia longispina (Kellicott) (Abb. 18). Das Verteilungsbild dieser Art weist zwei Maxima auf. Das erste hat eine ähnliche Lage wie die Konzentration der Crustaceen, nämlich im oberen Teil des Metalimnions der westlichen Seite des Sees. Aber eine andere, viel stärkere Anhäufung wurde am östlichen Ufer im Epilimnion beobachtet. In der Mitte war eine bedeutende Verminderung der Tieranzahl zu bemerken. Nach der Tiefe zu verminderte sich die Anzahl stark, und nur vereinzelte Tiere kamen im Hypolimnion vor. Hier bestand ein Teil der Tiere aus neu ausgeschlüpften, weichen *Kellicottia.* Ebenso stark verminderte sich die Menge in der Vegetationszone. Das Maximum war 1092 Tiere per 10 L.

Eine nähere Betrachtung dieses Verteilungsbildes veranlasst uns anzunehmen, dass hier eine direkte Korrelation zwischen Turbulenzströmungen und Anhäufungen von *Kellicottia* vorliegt. In der Mitte des Sees, resp. im Querprofil, wurde das Wasser zusammen mit den Planktonorganismen zum zentralen Seebecken hingetrieben. Die *Kellicottia* kämpfte zum Teil gegen die

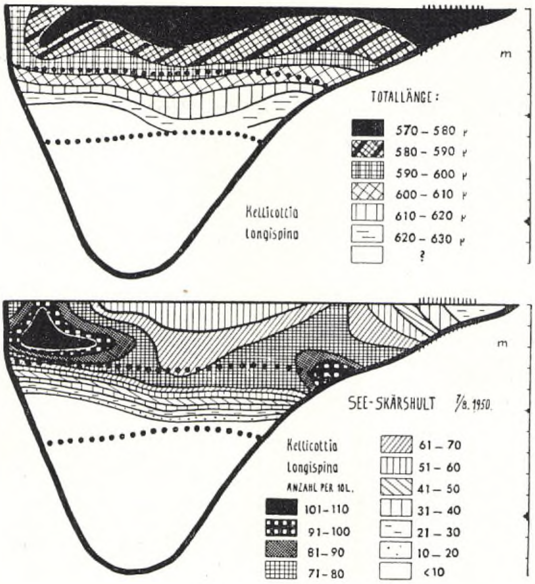

Abb. 17—18.

schwache Strömung an und bildete die unterbevölkerte Partie im mittleren Teil des Sees.

Die Tiere sammelten sich in der Ufernähe, wo die walzenförmigen Turbulenzströmungen sie hinsaugten. Solche Verschiebungen der Tierkonzentration werden noch stärker bestätigt, wenn wir die Gesamtlänge der *Kellicotta longispina* (Körperlänge+occipitaler Stachel+posteriorer Stachel) analysieren (Abb. 17). Untersuchungen einer grossen Anzahl von *Kellicottia* aus verschiedenen Seen zeigen häufig, dass diese in den oberen Schichten von kleinerer Grösse ist und dass die Mittelwerte nach der Tiefe zu ansteigen. Eine Auswertung dieser Ergebnisse wird an anderer Stelle mitgeteilt werden. Hier interessiert uns nur die Verteilung in den Turbulenzverhältnissen im Skärshult-See. Auch hier befinden sich die kleineren Tiere (Mittelwerte) im obersten Teil des Epilimnions, und die mittlere Grösse steigt je tiefer die untersuchte Schicht liegt. Aber tiefer vermindert sich die Anzahl der Tiere so stark, dass es genügt nicht mehr mit Individenanzahl, wenn sie sich etwas unterhalb von Metalimnion befinden. Diese Messungen zeigen ein Abweichung von der horizontal liegenden Schichtung; an einigen Stellen werden die Tiere nach oben gezogen. Dies tritt am klarsten am östlichen Steilufer in Erscheinung, wo auch eine Saugwirkung nach unten besteht, welche hier die kleineren Oberflächentiere in die tieferen Regionen verdrängt.

Es zeigt sich, dass die Messungen der Konzentration von *Kellicottia longispina* zusammen mit der Grössenanalyse uns ein Mittel zu einem detaillierten Studium der schwächeren Turbulenzströmungen gibt.

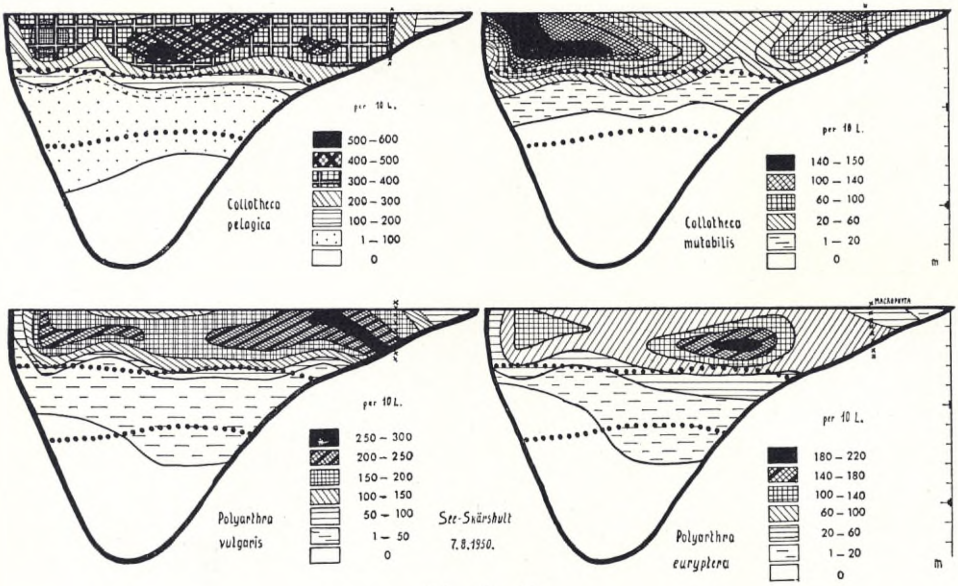

Abb. 19—22.

Keratella cochlearis cochlearis (GOSSE) (Abb. 15). Der Totalanzahl nach folgt die Art der vorhergenden, und weist als Maximum 582 Ind./ 10 L auf. Die Verteilung liegt im Epi- und Metalimnion. Die beiden Anhäufungen liegen am östlichen Ufer im Epilimnion, wobei die eine mehr zur Seemitte verschoben ist. Auch dies erklärt sich aus dem Einfluss von Turbulenzströmungen.

Keratella cochlearis hispida (LAUTERBORN). Diese Form wurde in geringerer Anzahl im Epilimnion an den verschiedenen Beobachtungspunkten gefunden.

Keratella hiemalis CARLIN (Abb. 15). Diese Winterform kam nur im unteren Hypolimnion vor und da nur in wenigen Individuen. Es muss angenommen werden, dass diese Tiere auch im sauerstoffarmen Wasser leben können, denn die Sauerstoffsättigung war hier nur 0,4 oder 0,6 %, also eine wenig von Sauerstoffsättigung beeinflusst stenök. Kalltwasserform.

Collotheca pelagica (ROUSSELET) (Abb. 19). Diese Art war reichlich im Epilimnion vertreten. Sogar in der Zone der Nymphaeiden wurde sie reichlich angetroffen, jedoch befanden sich in der Zone der Helophyten nur wenige Exemplare. Nur wenige waren auch im Metalimnion oder im oberen Hypolimnion verstreut. Eine Konzentration war in der Mitte des Epilimnions vorhanden. Dagegen wurde ein individuenarmes Wasser mit wenigen nach oben geschobenen *C. pelagica* am östlichen Ufer beobachtet.

Collotheca mutabilis (HUDSON) (Abb. 20). Diese Art unterliegt dem gleichen Einfluss durch die Strömungen wie *C. pelagica,* jedoch ist die Verteilung der

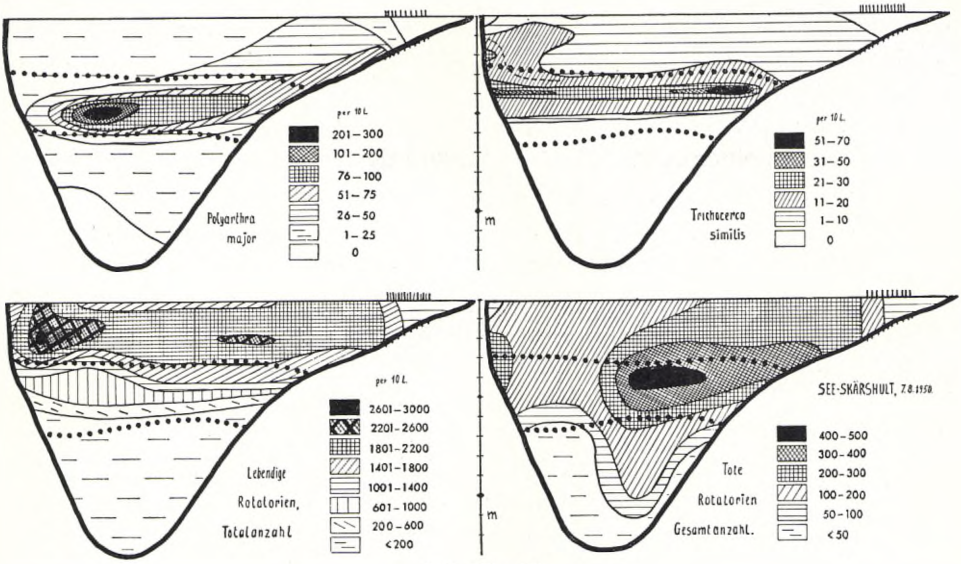

Abb. 23—26.

Anhäufungen markant unterbrochen durch eine dazwischen liegende Zone mit sparsamer Verbreitung. Ihre Hauptkonzentration liegt am östlichen Ufer, eine kleinere kurz ausserhalb der westlichen Vegetationzone. Eine sparsame Verteilung kommt auch im Metalimnion vor.

Collotheca libera (ZACHARIAS). Die Art ist in geringer Individanzahl nur im Epilimnion und eine kleinere Anzahl sogar in der Pflanzenzone angetroffen worden.

Polyarthra vulgaris CARLIN (Abb. 21). Die Verteilung dieser Art beschränkt sich auf das Epilimnion, wo sie hauptsächlich vor den Vegetationen gesammelt war. Ein kleinerer Teil befindet sich am östlichen Ufer. Eine Einwirkung der Turbulenzströmungen ist sichtbar. *P. vulgaris* geht auch in das Metalimnion hinein.

Polyarthra euryptera WIERZEJSKI (Abb. 22). Das Verteilungsbild ähnelt sehr dem von *P. vulgaris,* wenn auch die Individuenanzahl hier kleiner ist.

Polyarthra major BURCKHARDT (Abb. 23). Diese Art weist ein eigentümliches Verteilungsbild auf, weil die Tiere im Metalimnion konzentriert sind. Nur sparsam gehen diese Rädertiere ins Epilimnion oder in das Hypolimnion hinein. Man könnte annehmen, dass diese Art versucht, dem warmen Oberflächenwasser und ebenfalls dem sauerstoffarmen Tiefenwasser auszuweichen.

Polyarthra remata SKORIKOV (Abb. 13). Diese Art hat ein epilimnisches Ausbreitungsgebiet, geht auch in ziemlich reichlicher Anzahl in die Vegetationszone hinein.

Polyarthra longiremis CARLIN (Abb. 13). Sie ist eine hypolimnische Art, die niedrigem Sauerstoffgehelt auszuweichen sucht, da sie sich im oberen Teil des Hypolimnions ansammelt. Sie bevorzugt also kaltes Wasser bei nicht zu niedrigem Sauerstoffdruck.

Asplanchna priodonta GOSSE (Abb. 14) und *Asplanchna herricki* DE GUERNE. Diese beiden Arten sind im Pelagial des Epilimnions und im oberen Metalimnion verbreitet. Doch sieht die Verteilung ungleichmässig aus.

Conochilus unicornis ROUSSELET und *Conochilus hippocrepis* (SCHRANK). Die erstgenannte Art hat im Pelagial des Epilimnions ihre Verbreitung, doch geht sie auch in die Pflanzenzone hinein. Die maximale Anzahl war 110 per 10 L. Hingegen war die zweite Art nur in wenigen Exemplaren am östlichen Ufer vertreten.

Ploesoma hudsoni (IMHOF): Warmwasserform, zerstreut im oberen Epilimnion, weniger in der Pflanzenzone.

Trichocerca similis (WIERZEJSKI) (Abb. 24). Ebenso wie *Polyarthra major* ist diese Art auf das Metalimnion beschränkt. Nur wenige Tiere kamen auch im Epilimnion vor. Das aufsteigende Tiefenwasser hat am Gabrielsberget einen Teil in das Epilimnion mitgebracht.

Trichocerca capucina (WIERZEJSKI & ZACHARIAS). Epilimnisch wurde diese Art in geringer Anzahl bis in 4 m, meistens aber in 2 m Tiefe angetroffen (Warmwasserform).

Trichocerca rousseleti (VOIGT). Die Art wurde im Epilimnion in relativ geringer Anzahl angetroffen. In der Nähe der Vegetation wurde ein Maximum von 30 St./ 10 L festgestellt.

Gastropus stylifer IMHOF. Ein planktisches Rädertier, welches häufiger in Pflanzennähe sein Gebiet hat. Viel spricht dafür, dass diese Art als Warmwassertier angesehen werden kann, was auch aus dem Verteilungsbild des Skärshult-Sees zu ersehen ist. Hier wird es meistens in 2 m Tiefe angetroffen und geht höchstens bis 4 m hinunter. Aber wie kann man das Phenomen erklären, dass diese Tiere auch reichlich im Winter vertreten sind? Ich habe diese Tiere im Winter oft im Plankton der Fischteiche (Aneboda) gefunden, wo das Wasser 0° oder höchstens +2°C war. Ebenso war diese Art im Plankton von Förhult-See unter den Winterserien antreffbar.

Filinia longiseta (EHRENBERG) (Abb. 14). Diese Art ist sicher eine Kollektivart, wenn auch die bisherige Einteilung in einige Kleinarten nicht viel dazu beigetragen hat, ein sicheres Unterscheidungsmerkmal festzustellen. Sie wird als eutropher Rotator angesehen, was auch in den meisten Fällen wohl mit der Mehrzahl der Beobachtungen übereinstimmt. Etwas unklar ist hierbei aber das Auftreten von *longispina* auch in oligotrophen oder sehr schwach eutrophierten Seen. Sie kommt dann jedoch fast ausschliesslich im Winter oder, wie in unserem Skärshult-See, nur im kalten Tiefenwasser vor.

Ascomorpha ecaudis PERTY, *Ascomorpha ovalis* (BERGENDAL) und *Ascomorpha saltans* BARTSCH. Diese Arten kamen pelagisch im Epilimnion vor, doch nur *A. ovalis* in etwas grösseren Individenanzahl (Maximum 25 St./ 10 L), während die anderen weniger verbreitet waren.

Synchaeta oblonga EHRENBERG. Verbreitet im Epilimnion, geht auch in die Vegetationszone hinein. Ziemlich sparsam verteilt, mit einer Maximalanzahl von 29 Ind./ 10 L bei Stat. 3.

Die anderen beobachteten Arten waren zu wenig vertreten, um etwas über die Verteilung im Querprofil sagen zu können.

Mortalität

Nicht nur die Verteilung der lebenden Rotatorien (Abb. 25), sondern auch der Grad des Absterbens der verschiedenen Arten wurde analysiert. Das Verteilungsbild der abgestorbenen Rotatorien der ganzen Gruppe ist auf dem Diagramm angegeben ((Abb. 26). Die gestorbenen Tiere ergaben 12,6 % der totalen Anzahl der lebenden und toten Rädertiere zusammen, auf jede siebente lebende Rotatorie im Profil kam also ein totes Tier.

Es ist möglich, dass die ganz weichen Arten, wie *Collotheca* u.a., sich sofort nach dem Absterben auflösen; dagegen schweben die stärker gepanzerten und mehr stacheligen Tierreste viel länger im Wasser, was man aus den untersuchten Proben vermuten konnte. Den höchsten Prozentsatz an toten Individuen wiesen *Trichocerca capucina* gefolgt von *Keratella c. cochlearis, Polyarthra*-Arten, dann weiter *Kellicottia* und *Trichocerca similis* auf. Die Anzahl der gestorbenen Tiere im Plankton war bei den dominanten Arten nicht am grössten.

Tabell IV. Die lebenden und toten Rotatorien im Querprofil.

Arten der Querprofile	Individanzahl in % bei allen lebenden Rotatorien	Die toten in % der gesamten abgestorbenen Tiere	Eventuelle Stufe des Absterbens
Kellicottia longispina	39,3	41,8	13,5
Keratella c. cochlearis	21,6	34,2	18,6
Collotheca pelagica	14,0	0	0
Polyarthra vulgaris	6,5	13,4[1]	16,9[1]
Collotheca mutabilis	4,0	0	0
Polyarthra euryptera	3,3	5,1	17,9
Polyarthra major	2,3	[1]	[1]
Polyarthra remata	1,6	2,2	15,7
Asplanchna priodonta	1,3	1,2[2]	10,9[2]
Conochilus unicornis	1,0	0	0
Polyarthra longiremis	1,0	[1]	[1]
Trichocerca similis	0,7	0,7	11,8
Gastropus stylifer	0,5	0	0
Trichocerca rousseleti	0,5	0,2	6,5
Ascomorpha ovalis	0,5	0,05	0,9
Synchaeta oblonga	0,4	0,05	1,5
Collotheca libera	0,3	0	0
Trichocerca capucina	0,2	0,5	22,5
Asplanchna herricki	0,2	[2]	[2]
Lepadella patella	0,1	0,05	5,6
Ploesoma hudsoni	0,1	0	0
Filinia longiseta	0,1	0	0

[1] Anzahl der toten gemeinsam für alle *Polyarthra*-Arten.

[2] Anzahl der toten gemeinsam für beiden *Asplanchna*-Arten.

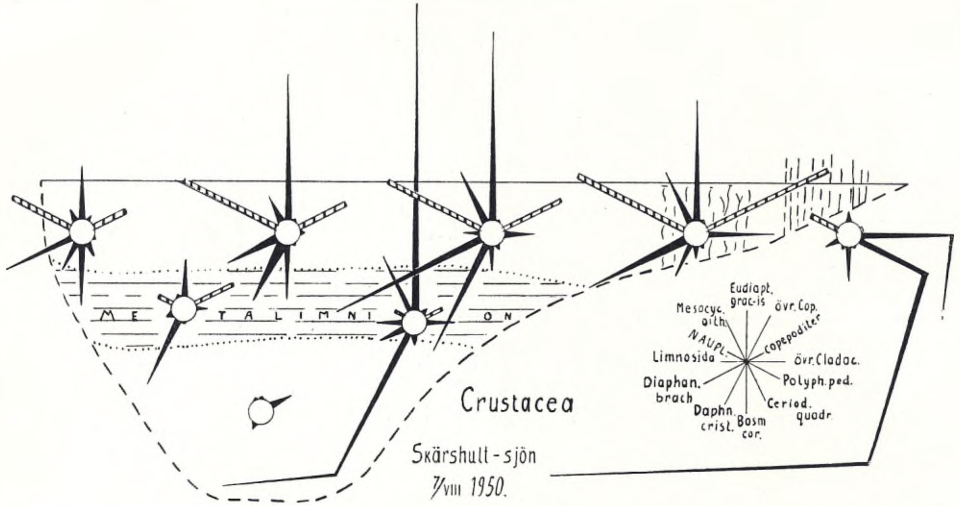

Abb. 27. Die Verteilung (in Prozent) von Crustaceen in den verschiedenen Schichten. Nauplien und Copepoditen separat gerechnet.

Zusammenfassung über das Querprofil

Die Untersuchungsresultate zeigen, dass das Verteilungsbild in erster Linie von physikalisch-chemischen Umweltsfaktoren beeinflusst wurde, wobei die Arteigenschaften der verschiedenen Tiere sekundär mit ihren biologischen Reaktionen mitgewirkt haben.

Betreffend der Milieufaktoren sollen zuerst Temperatur, Sauerstoffdruck und Lichtintensität als sehr wirksame Elemente hervorgehoben werden. Hinzu kommt die Einwirkung des Windes durch Turbulenzströmungen im Epilimnion und nur teilweise auch im Metalimnion. Als biologisch meist wirksamer Faktor auf die Verteilung sollen Phototropismus und die Möglichkeit, mit eigenen Kraftansträngungen gegen die Strömungen zu arbeiten, erwähnt werden. Für *Copepoda* und *Cladocera* hat das negative Phototaxis eine grosse Bedeutung, weil dieses die vertikalen Wanderungen verursacht. In unserem See hat die thermische und chemische Schichtung (und Stabilität) die Richtung beeinflusst, da die Versuche nach unten zu gehen, zu einer Anhäufung am westlichen Ufer, an dem mehr beschattete Stellen vorkamen führte. In ihrem Bestreben, in die Tiefe zu kommen, waren die Tiere gezwungen, den kälteren, sauerstoffärmeren Wasserschichten auszuweichen. Nur einige Arten haben ein spezielles Verbreitungsbild, in dem sie sich die ganze Zeit im Hypolimnion aufenthalten, wie dies bei *Cyclops s. strenuus* der Fall ist. Die Copepoditen werden auch von Strömungen mitgerissen, wie dies das Querprofil an der östlichen Seeseite zeigt. Es ist anzunehmen, dass die Nauplien viel weniger gegen Strömungen arbeiten können, aber im Skärshult-See kommt

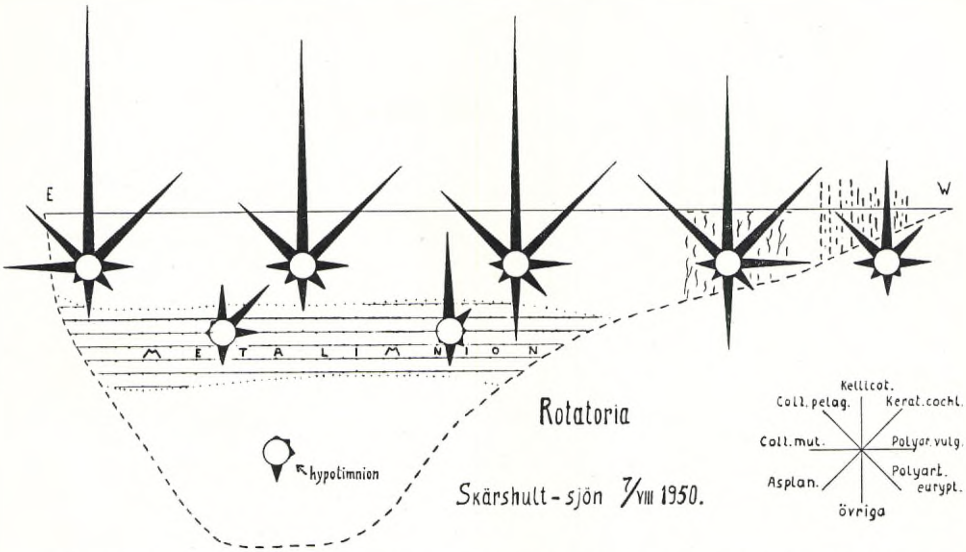

Abb. 28. Die Verteilung (in Prozent) von Rotatorien in den verschiedenen Schichten.

dies nicht besonders deutlich zum Vorschein, weil die Konzentration an und in der mehr geschützte Vegetationszone gelegen ist, und es ist nicht sicher, ob die Nauplier sich nicht auch zu anderen Tageszeiten gleich verhalten.

Die Rotatorien erlauben es einige Schichtungstypen zu erläutern. Wenn auch diese Tiere meistens mit Strömungen fortgetragen werden, haben einige auch die Möglichkeit sich gegen schwächere Strömungen vorzuarbeiten. Zuerst können wir eine Gruppe von Arten nennen, welche nur im Epilimnion vorkommt, oder höchstens etwas in das obere Metalimnion hineingeht. Als solche Arten können wir alle 3 *Collotheca*-Arten nennen, auch *Trichocerca capucina, Gastropus stylifer, Polyarthra remata* u.a. Ein etwas abweichendes Verteilungsbild weisen die epilimnische Arten auf, welche auch reichlicher im Metalimnion vertreten sind, wobei einige manchmal sogar in das obere Hypolimnion eindringen. Solche sind z.B. *Kellicottia longispina, Keratella c. cochlearis* und *Polyarthra euryptera.*

Ein markanteres Verteilungsbild weisen die Arten auf, die eine ganz enge Verbreitung im Metalimnion haben. Als solche sollen *Polyarthra major* und *Trichocerca similis* genannt werden.

Die extremsten Regionen weisen die Arten auf, welche niedrige Temperaturen zusammen mit niedrigem Sauerstoffgehalt bevorzugen, nämlich *Polyarthra longiremis, Filinia longiseta,* und *Keratella hiemalis.* Man kann annehmen, dass hier der Hauptgrund in der niedrigen Temperatur liegt, weil diese Arten sonst in der Winterzeit im sauerstoffreichen Wasser vorkommen.

Die Tieren, welche eine eigene, ziemlich starke Lokomotionskraft haben (*Copepoda, Cladocera*) können uns nicht viel über die kleineren Turbulenzströmungen berichten. Dagegen können die weniger kräftige Rotatorien, besonders *Kellicottia longispina* mit ihren Grössenverhältnissen über die kleinsten Wasserbewegungen Auskunft geben, da wir ein Hilfsmittel haben, welches uns erlaubt, die Bildung von Wasserwalzen in Ufernähe zu studieren. Damit können wir auch die Entstehung von Planktonwolken durch Saug- und Transportwirkung erklären.

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Some New Observations on the Spawning Behaviour of the Pike, *Esox lucius* L

By Eric Fabricius and Karl-Jacob Gustafson

Contents

1. Introduction

Field observations on the spawning behaviour of the pike have been made by several authors, for example by Mc Namara (1937) and Clark (1950). As the observation of the details of the spawning movements in the field proved very difficult, it was felt that aquarium experiments would be helpful. Some preliminary experiments, carried out at the Institute of Fresh-Water Research at Drottningholm, showed that it is not difficult to bring the pike to spawn in aquarium tanks, provided these are large enough. One of these early experiments was described by Lindroth (1945, p. 104), and another by Svärdson (1949 a).

In May 1956 a series of more extensive experiments were made in which we used two aquarium tanks. The larger of these had a bottom area of 700 by 80 cms, whereas the bottom area of the smaller tank, which was mainly used for photographing, was 215 by 57 cms. In both tanks the depth of water was maintained at between 40 and 50 cms. The pike used in these experiments were spawners brought from Lake Mälaren. The spawning of 16 females, some of which spawned with several males, was watched in the aquaria, and we were able to make detailed observations on some hundred spawning acts. 54 spawning acts were recorded on 16 mm. ciné film (Kodachrome), and of these records 15 were taken at slow motion (64 frames per second) and 39 at normal speed (32 frames per second).

In addition to the aquarium experiments, field observations were made in the spawning area within the grounds of the Institute (Lake Mälaren). For the field observations we used polarizing spectacles which eliminated much of the reflections from the water surface.

2. Exploratory and Agonistic Behaviour

The most favoured spawning ground for pike at Drottningholm are flooded meadows of sedge grass, between the shoreline and the belt of Phragmites-reed. At the beginning of the spawning season single pike, most of them males, are seen moving about within the spawning grounds, particularly during sunny days. Most of them are found in places, where the water is warmed up by the sun, and they seem to avoid colder water, for example in the shadow of trees, or in places subject to wind. These pike swim slowly, in an exploratory way, mostly parallel with and close to the shore, and they often penetrate into water so shallow that the back of the fish becomes visible over the surface. Now and then they rest, sometimes for hours, in depressions between the tussocks. These resting places can not be regarded as the centres of territories, since the fish do not regularly return to them, and when with the movement of the sun a tree casts its shadow over the place, the pike often abondons it, and moves to another site. During the course of a day these pike may travel over considerable distances along the shore.

In the aquaria it was observed that the pike during this exploratory behaviour carried out intense eye movements, indicating that they were searching for some visual stimuli. In the big tank some experiments were made in which about half the bottom area was covered by a carpet of spruce-fir, while the other half of the bottom was left bare. Males as well as females showed a clear preference for the mat of fir, concentrating mainly in that part of the tank.

If two of the males happen to meet, one of them often turns, and swims away in an opposite direction. At the spawning grounds these encounters were sometimes accompanied by a splash, but it was not possible to follow the events in detail. The aquarium observations revealed that on approaching each other the pike often adopt a characteristic threat posture (fig. 1), in which the branchiostegal membrane is lowered, the back is arched, and the maximally expanded paired fins point downward, and are kept in their foremost position, while the mouth is slightly opened. The erection of the paired fins occurs only at the highest intensity level of the threat posture, while the gill membrane display and the arching of the back are seen also at low intensity levels.

During this display the fish sometimes glides forwards by slow swimming

Fig. 1. Male pike performing the threat display in front of an opponent. Note the arching of the back, the opening of the mouth, the lowering of the branchiostegal membrane, and the erection of the paired fins. The two dark bars in the eye region are visible in the threatening male as well as in the specimen to the left. These specimens, as well as those shown in Figs. 2—6, had received some injuries in the mouth, when caught in the fyke nets. — Photogr.: K.-J. Gustafson.

movements, and often orientates itself so that the flank is turned towards the opponent. The threat posture thus has the character of a lateral display. Unripe females were also often seen adopting the threat posture on the close approach of another pike, male or female. The threat display is not restricted to the spawning season. It occasionally occurs during the non-reproductive seasons as well, and is seen also in young pike, already during their first summer of life.

During more than 120 hours of aquarium observations, we have seen only two cases of actual attack in which a male rushed against another, and bit it in the flank. In one of these cases a big male attacked a smaller one which performed the lateral display in front of his nose, and the other case occurred on an occasion, when several males courted a single female. The biting was just a sudden nipping, and the attacker did not grip hold of its opponent. We could thus confirm the observations made by Mc Namara (1937) that pike actually fight on the spawning grounds, but apparently these cases of overt pugnacity are extremely rare in this species.

3. Courting

If two pike of opposite sex happen to meet, the male approaches the female, and courts it by rubbing its nose gently against the sides of the head and the anterior parts of the flanks of the female. The sexual approach of the male shows the variability typical of an appetitive behaviour. It may overtake the female from behind, or swim backward towards it from a position in front of it, and often the male is also seen approaching the female by a sideward movement, or by sinking or raising from a position above or below it, respectively. This variability of the sexual approach is not a self-evident feature of fish behaviour, for the male char, for example, almost invariably approaches the female from behind, by a forward swimming movement. Even if the female char should be in a position behind the male, it turns round and often swims past the female, making then a new turn, and swimming forwards towards it from behind (FABRICIUS 1953, FABRICIUS and GUSTAFSON 1954). In the pike, the sexual approach is not always made by the male only. We also observed some cases in which an active female approached a male, swimming up side by side with it.

When a courting male approached an unripe female, moving up side by side with it, the female often showed it off by a special movement. This behaviour was a jerky shaking of the head which could be repeated several times with intervals of some few seconds. An analysis of some slow motion pictures showed that the female suddenly turns its head laterally, towards the male, and then brings it back into the median position, but movement of the head is not continued to the opposite side. These movements present striking similarities to the short, jerky shaking movements of the head by which a pike that has caught a large fish turns this prey, until it can be swallowed (cf. WUNDER 1927, HOOGLAND, MORRIS and TINBERGEN 1957). For comparing these movements, we made slow motion records of a pike catching and swallowing a roach. An analysis of these records showed that even in this case the head is suddenly turned at first to one side and then back to the median position, but not to the opposite side, and that these movements are repeated several times, until the prey can be swallowed. This usually happens, when the head of the fish has been brought into the mouth cavity of the pike.

It seems possible that the head-shaking by which courting males are shown off by unripe females has originally been derived from "prey-turning-movements" which have occurred as a displacement activity in the conflict situation created in the female by the approach of a male. Movements belonging to the pattern of catching and swallowing a prey are known to occur as displacement activities in conflict situations in other species of fish, for example in salmonids (FABRICIUS 1953, FABRICIUS and GUSTAFSON 1954). As has been pointed out by several ethologists (cf. for example, TINBERGEN 1952 a), such derived activities are, more or less, changed or "ritualized" in the course of evolution. This has apparently also been the case with the head-shaking of the female pike. Thus, this activity lacks the "chewing" movements of the jaws which are characteristic of the true preyturning movements.

It could be observed that the head-shaking of the female really acted as a repulsive signal, the males very often responding to it by withdrawing from this particular female, and searching for a new one. It should be mentioned that the repulsive head-shaking is not shown by unripe females only. It also occurs, towards the end of the spawning, in females which begin to be almost void of eggs, but which are still courted by the males.

If the female does not show the male off by the repulsive head-shaking, or by rushing away, the male takes up a position, parallel to the female, and the two fish move forward side by side. During this courtship swimming, the male adjusts its position so as to maintain its eyes approximately on a level with the eye region of the female. The female also cooperates with the male in maintaining this mutual position of the two partners. Presumably this mutual orientation is facilitated by the fact that the pike has two distinct dark bars, one running from the eye straight down to the upper jaw, and another running straight forwards from the eye. The eye is thus located at the point of intersection of the two bars (Figs. 1 and 2). If the male is smaller than the female, as is the rule in the pike, this adjustment results in the genital opening of the male being, more or less, ahead of that of the female.

We could not confirm the observations by SVÄRDSON (1949 a), that the male assumes a position such as to touch with its pectorals those of the female. If the male was considerably smaller than the female, its pectorals were often so much ahead of those of the female that they did not touch them at all. Apparently the orientation of the two fish in relation to each other is mainly a visual adjustment in which the eye region and its conspicuous markings play an important rôle.

4. Spawning

While the two fish move forward during the courtship swimming, the male presses its body, and particularly the posterior part of it, against the female. The swimming movement is of the carangiform type (BREDER 1926) in which trunk and tail are undulated laterally. The intensity and amplitude of these undulations become increasingly greater, particularly in the region behind the pelvic fins. Finally the male by a sudden flap thrusts the pelvic region of its trunk against the female which at this mating thrust sheds a portion of eggs, while the male sheds a portion of milt. The milt is only visible under good lighting conditions, appearing as a very thin mist. The eggs are whirled about by the jet currents caused by the movements of the fish, but sink to the bottom within a few seconds. At first they roll about, but soon they become sticky, and adhere to plants and debris.

We could thus confirm the statement made by SVÄRDSON (op. cit.) that the mating thrust is always delivered by the male, and not, as was earlier supposed by LINDROTH (1946), by the female. In some other details SVÄRDSON's account is, however, contradicted by our observations. According to SVÄRDSON the male performed increasing swimming movements with his paired fins while pressing against the female's body, and the female responded by an equivalent increasing swimming movement of the fins, which in turn accelerated the male's movements. In this way their synchronous swimming "standstill" increased for one or more seconds, until their bodies began to vibrate, with all their fins participating. Finally the male emitted his milt with a violent flick of its abdomen and caudal fin against the female.

We could not see any conspicuous movements of the paired fins, except in some few cases, when a courting male approached a female by swimming backwards, and the female tried to avoid it by a backward movement. In these cases the fish swam backward by beating the paired fins at a slow rhythm. As described by HOOGLAND, MORRIS and TINBERGEN (1957) this is, however, a normal locomotory movement. The beating of the male's and the female's fins was not synchronous. These facts contradict the view of SVÄRDSON, viz. that the mutual synchronisation of the swimming locomotory actions was significant, and that the pectorals must have some releasing function, when moved. He was led to this conclusion in part by the observation that the male instantly stopped his action, if the female turned towards the glass of the aquarium, which disturbed the female, and caused it to stop its movements. We think, however, that the male was disturbed, because the collision of the female with the pane stopped her forward swimming, and forced her to turn, which made it necessary for the male to make a new adjustment of its position in relation to the female. Another reason for SVÄRDSON's opinion was his assumption that the male orientates itself in relation to the female so that their pectorals touch, but this assumption has, as already mentioned, been shown to be erroneous. During the spawning the paired fins of the pike, if used at all, are apparently only used in a normal locomotory way and do not seem to have any special releasing function in the sexual behaviour.

Also, we could never see a spawning couple "swimming standstill". In all the several hundred spawning acts observed by us the fish constantly swam forward during the courtship, and the female continued its forward swimming even during the actual mating. SVÄRDSON, who based his account on observations on the spawning of two couple of pike in an aquarium, observed in one case in the field a couple moving forwards during the spawning act, and therefore assumed that the swimming "standstill" in the tank might have been a modification due to the confined space. It is, however, interesting that the spawning pike always swam forward in our filming tank, though it had a bottom area of 215 by 57 cms, which is smaller than SVÄRDSON's tank, the bottom area of which was 230 by 80 cms.

Moreover, we could never see the vibrating of the body and fins, described by SVÄRDSON. Prior to the mating flap, the pike performed undulatory movements with the posterior part of the body, but these movements were not as swift as to give the impression of a vibrating or trembling. In any case, there is nothing like the real trembling, occurring, for example, in the courting and spawning of the char (cf. FABRICIUS 1953).

5. The series of spawning acts

As described by SVÄRDSON (op. cit.), the spawning of the pike consists of long series of mating acts, repeated with short intervals, and these series are separated by periods of rest. In the aquarium as well as in the field we observed that immediately after the mating act the two fish usually stop their forward swimming for some few seconds, hovering at a distance of approximately 10—30 cms from each other, but very soon the male again approaches the female, and the couple starts swimming forward side by side for the next mating act in the series.

Within the series of mating acts, we found an average of 1.5 to 2.6 acts per minute in the aquarium observations at a water temperature of +18°C, and 1.7 acts per minute in the field observations, when the water temperature at the spawning grounds was +12°C. These figures fairly well agree with the observations made by SVÄRDSON who found that the spawning acts within each series were repeated every minute or so, but they indicate a greater intensity of the spawning than that found by CLARK (1950) who noted that spawning took place every 3 to 5 minutes. Probably, however, the observations by CLARK were made not only within the series of mating acts, but must have included also the intervals between the different series, or at least some of the shortest of these intervals.

As shown by Table 1 the length of each series of mating acts as well as the number of acts included in each such series was comparatively small at the beginning of the spawning of a couple. It then rapidly increased, in order finally to decrease again towards the end of the spawning. It is a well known fact that this initial increase and final decrease of intensity is characteristic of very many instinctive activities (cf. for example, LORENZ 1950 and others).

As a rule, the intervals between the different series of mating acts lasted 1—40 minutes. Timing of a series of 12 such intervals gave an average of 7.9 minutes. In some cases, however, we observed longer intervals, lasting about one hour or more. During the intervals male and female were often seen resting upon the bottom, at some distance from each other, but they

Table 1. The approximate length of each series of spawning acts and the number of acts included in each series during the spawning of a couple of pike in an aquarium.

Series No.	Length of each series, in minutes	Number of acts
1	2	2
2	2	3
3	4	6
4	3	8
5	7	7
6	5	8
7	7	13
8	11	9
9	6	8
10	1	3
11	2	5

could also swim slowly about, without showing any interest in one another, and the males could be involved in aggressive encounters with other males. Towards the end of the spawning of a couple the length of the intervals increased. This is well in accordance with the fact that repeated release of an instinctive activity temporarily reduces the ability of the animal to respond to the sign stimuli which release this particular activity (cf. for example, LORENZ 1950 and TINBERGEN 1951), and this increase of the refractory period after repeated sexual performance has recently been proved statistically by LARSSON (1956) for the male albino rat.

For filming, couples which had begun their spawning in the big tank were transferred to the smaller photographing tank, and during periods, when we had no time to watch them, males and females were kept separated in other tanks. This frequent transfer of the fish from one tank to another made satisfactory statistics on the total length of the spawning impossible. In two cases, however, a couple was allowed to spawn without disturbance, and their spawning lasted 5 hours 40 minutes, and 1 hour 11 minutes, respectively. These experiments as well as the experiments on the length of the intervals between the mating acts were made in the smaller tank, where the water temperature was +18°C.

It should, however, be mentioned, that the females used in the aquarium experiments were, for natural reasons, comparatively small, none of them measuring more than about 50 cms in length. It seems probable that larger females need a considerably longer time in order to shed all their eggs. The spawning is also lengthened by the fact that the pike do not spawn during the night. Females which had started their spawning in the evening always interrupted it as soon as it grew dark, resuming the spawning activities in the following morning. Another important circumstance is found in the reduction of the spawning intensity by spells of cold. Thus it seems probable that the spawning of large females might be distributed over several successive days.

In the big tank a couple of spawning pike was observed to move forward about one meter between each successive mating act in a series. If there are about 1.5 mating acts per minute within the series, and if the average length of the series is about 5 minutes, this would mean that within each series the pike perform about 7.5 mating acts, and move forward for about 6.5 metres. The average duration of the intervals between the separate series, about 8 minutes, would allow the occurrence of about 5 series per hour, and this would mean that the spawning couple would travel forward about 32.5 metres per hour. If the highest observed frequency of mating acts, 2.6 per minute, is used as a basis for this calculation, the result would be 60 metres per hour. In the field we have observed cases in which a couple of spawning pike travelled over considerably longer distances per hour, up to about 200 metres. One of the reasons for this is probably the patchy distribution of the optimal bottom on the natural spawning grounds. The pike do not perform any mating acts while swimming over unsuitable areas. They rapidly pass over these areas, thus increasing the distance travelled per hour. Moreover, in the field observations the movements of the observer could in some cases have frightened the fish, causing them to swim forward more than they would have done if undisturbed. In the aquarium the pike were not at all disturbed by slow movements of observers outside the front pane.

6. Formation of spawning groups

In the field observations we could confirm the statement made by CLARK (1950) to the effect that most of the spawning groups were composed of 2—3 males and one female, while groups consisting of one male and one female were comparatively rare. In groups of 2 or 3 males and one female it was observed, in the field as well as in the big tank, that the mating thrusts were delivered now by one and now by another of the males, which swam on either side of the female.

However, the frequency of mating acts per time unit was of about the same magnitude as with single pairs. This seems to indicate that the behaviour of the female is of essential significance in determining the frequency of mating acts. Sexually active females respond to the approach of a courting male by starting a slow forward swimming movement. The male follows, swimming side by side with the female as described in chapter 4, and this behaviour terminates in a mating act.

In the experiments described by SVÄRDSON (1949 a) only one male attended the female, and spawned with it, though two males were present in the tank. In our big tank, however, spawning groups of two males attending the same female were observed on several occasions, but in our smaller tank we never observed more than one male spawning with a female, though up to 4 males were often present in this aquarium. In this small tank the largest or most active male repeatedly made aggressive approaches to the other males, and threatened them, particularly during the intervals between the series of mating acts. While a couple was spawning, another male sometimes happened to make an attempt at attending the female, but the dominant male immediately showed him off by pushing against his flank, performing the threat display, or by turning his head against him. As the confined space prevented the other males from avoiding the frequent attacks of the dominant male, they were soon intimidated, and did not show any more attempts at taking part in the spawning. Apparently the permanent sight of the dominant male made any sexual activity impossible for them.

In the big tank the other males simply swam away from an aggressive male, and were after this still able to show sexual activity on meeting a female in another part of the tank, where the antagonist was not visible for the moment. In the cases, when two males attended the same female, mutual threatening occurred between them during the intervals between the series of mating acts, and one of them could make an avoiding manoeuvre, but as soon as the next spell of sexual activity began, both of them again joined the female.

The possibility of avoiding the aggressive specimens seems to be the main reason, why the weaker males are not permanently intimidated in big tanks and in the field. In really territory-guarding species of fish, it is not possible for an intruding male to approach the female of the owner of a territory without penetrating into the centre of the territory, where the aggressivness of the resident male is so intense that the trespasser is almost always driven off. For example, when this same big tank was used for spawning char, it was soon divided into a number of distinct territories, each of which was permanently defended by a spawning couple (FABRICIUS and GUSTAFSON 1954). The spawning pike, however, swam about at random in all parts of the tank, where suitable bottom material was present. Sometimes two or more couples spawned simultaneously, and on swimming about during their spawning activities these couples repeatedly met, now here and now there in the tank, but no aggressivity between the different couples was seen at these encounters. Such a behaviour would not be possible in a territory-guarding species.

A successive polygamy was frequently observed in the males. They abandoned the females as soon as these were spent, starting new series of spawning activities with some other female. In the big tank it was also observed that a male could abandon his female during one of the intervals between the series of mating acts, starting his next series of mating acts with a new female, while the first female could spawn again, but now with another male.

This frequent exchange of partners seems to indicate that there is no real pair formation in the pike.

Finally it should be mentioned that some cases of homosexual behaviour have also been observed. It frequently occurred that a male made a sexual approach to another male, swimming up side by side with it, and rubbing its nose against the other's head. In most cases the approached male either fled or showed the sexually active male off by adopting the threat posture. In some instances, however, a mutual sexual behaviour ensued. The approached male responded by moving slowly forward, like a ripe female, and during some minutes the two fish swam side by side in the manner characteristic of the courtship swimming of a normal heterosexual couple. In one of these cases a small male, that had approached a larger male, even performed a series of spawning flaps. Most probably this homosexual behaviour, which occasionally occurs in the pike, is of the same type as that observed in the char, i.e. it is just a consequence of the fact that features which are shared by males and females represent some of the sign stimuli releasing the sexual behaviour of the male (FABRICIUS 1953). In the ten-spined stickleback MORRIS (1952) has described another type of homosexuality in which dominating males show the male behaviour pattern, while dominated males show the female pattern.

7. An Analysis of the Mating Act

The movements of the spawning pike are very rapid. Even though slow-motion records with 64 frames per second were used, the minute details of the movements could not be perceived, when the film was run through the projector at normal speed. For analysing the details of the movements it proved necessary to use a moviscope in which the frames of the film could be studied one by one. By using this method we could distinguish the following three stages in the mating act:

1. The first sign indicative of a following mating act is the lowering by the male of the branchiostegal membrane. The white colour of this membrane, contrasting sharply with the dark colour of the rest of the head, makes this display very conspicuous, and it should be remembered that during the courtship swimming this region of the male's head is held very close to the eye of the female. The female often responds by a corresponding lowering of its branchiostegal membrane, and the two fish increase the intensity of the undulatory movements of the posterior parts of their trunks and the speed of their forward swimming. During this rapid swimming, the male, by bending its trunk very sharply towards the female in the region of its own dorsal and anal fins, suddenly delivers a powerful tail flap against the female (Fig. 2). This initial flap is not accompanied by any ejection of sexual pro-

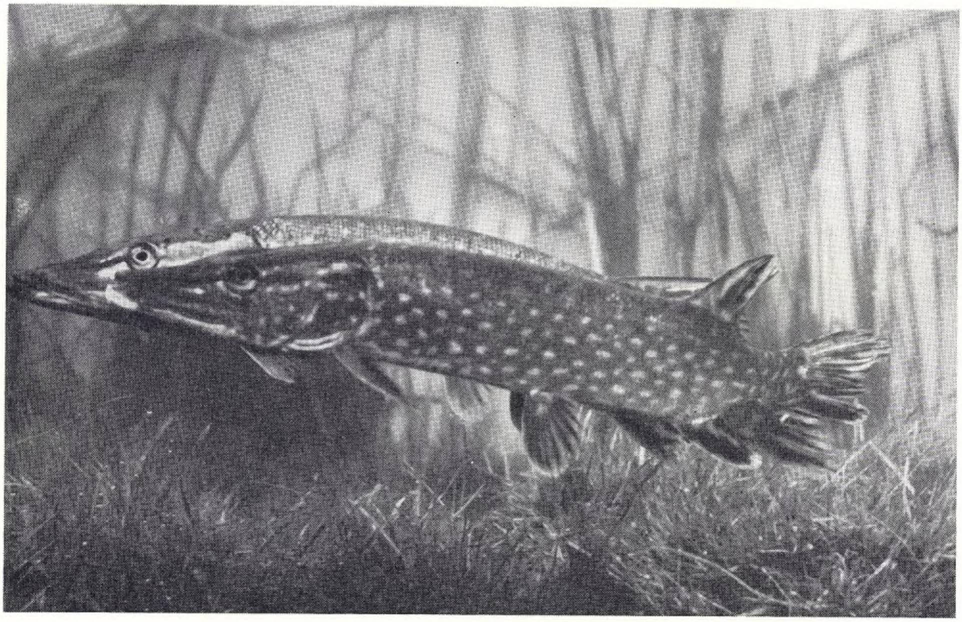

Fig. 2. Male pike (nearest the pane) performing the introductory flap. The branchiostegal membrane is lowered, and the caudal part of the body is bent towards the female. — Photogr.: K.-J. Gustafson.

ducts. In the slow motion pictures, taken at a speed of 64 frames per second, this initial stage, from the lowering of the branchiostegal membrane to the completion of the tail flap, covered 8 to 12 frames, which means that its actual duration must have been, roughly, between 0.1 and 0.2 seconds. Sometimes two successive initial flaps were delivered, in which case this stage covered about 28 frames, but as a rule only one initial flap occurred.

2. After the initial flap the male turns its tail away from the female, moving it suddenly to the other side. This movement is continued in such a way that the tail fin of the male beats sideward, and finally forward, thus exerting a strong backward pull on the body, with the result that the forward movement of the male is suddenly arrested and gives way to a backward movement. The braking effect of the tail stroke is supported by movements of the pectoral and pelvic fins. As soon as the tail stroke begins, these paired fins are erected as much as possible and turned to their foremost position. During the rest of "stage 2" they are then maintained motionless in this stiff and erected condition (Fig. 3).

While the tail fin of the male strikes in a direction away from the female, the bending point of the male's trunk travels forward, and the bend becomes very sharp. As a consequence, the region of the genital opening of the male hits the corresponding region of the female with a powerful thrust. This is

Fig. 3. The onset of the braking stroke. The tail fin of the male is moved in a direction away from the female, and beats forwards, while the paired fins are erected, and the lowering of the branchiostegal membrane reaches its maximum. — Photogr.: K.-J. Gustafson.

Fig. 4. The mating thrust. The region of the genital opening of the male hits the corresponding region of the female, causing a bending of the latter's body. The head of the male is bent towards the female, and its mouth is opened. — Photogr.: K.-J. Gustafson.

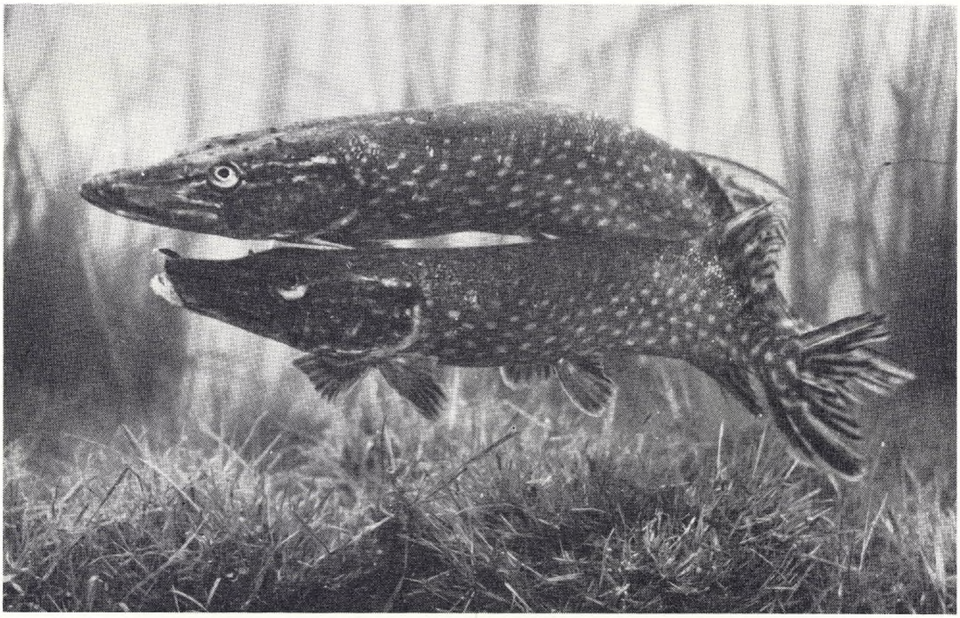

Fig. 5. The female has been thrown sidewards and upwards by the powerful mating thrust of the male. The paired fins of the male are still erected, and its anal fin is bent towards the female. — Photogr.: K.-J. Gustafson.

the actual mating during which the male ejects his milt. Simultaneously, a compensatory bending of the trunk in the opposite direction appears in the region between the pectoral and pelvic fins, resulting in a sudden turning of the head of the male towards the head of the female. During this turning of the head the male slightly opens his mouth. At this stage the trunk of the male forms an "S", with the head towards the female and the tail away from it, and body of the male is rotated so that his belly is turned towards the female (Fig. 4).

The movements from the onset of the braking stroke of the male to the completion of the mating thrust covered 6 to 13 frames of the slow-motion film. During the first phases of these movements the female swam forward without showing any bending of the trunk or other conspicuous movements, until it was hit by the genital region of the body of the male. Exactly at this moment the female suddenly erected its pelvic fins to a maximum, but immediately moved them back to their normal position, and simultaneously its trunk became more and more bent, finally forming a "J", with the tail part turned towards the male (Figs. 4—5 and 7 a—e). The erection and subsequent flattening of the pelvic fins was so rapid that it covered only 3 to 4 frames of the film.

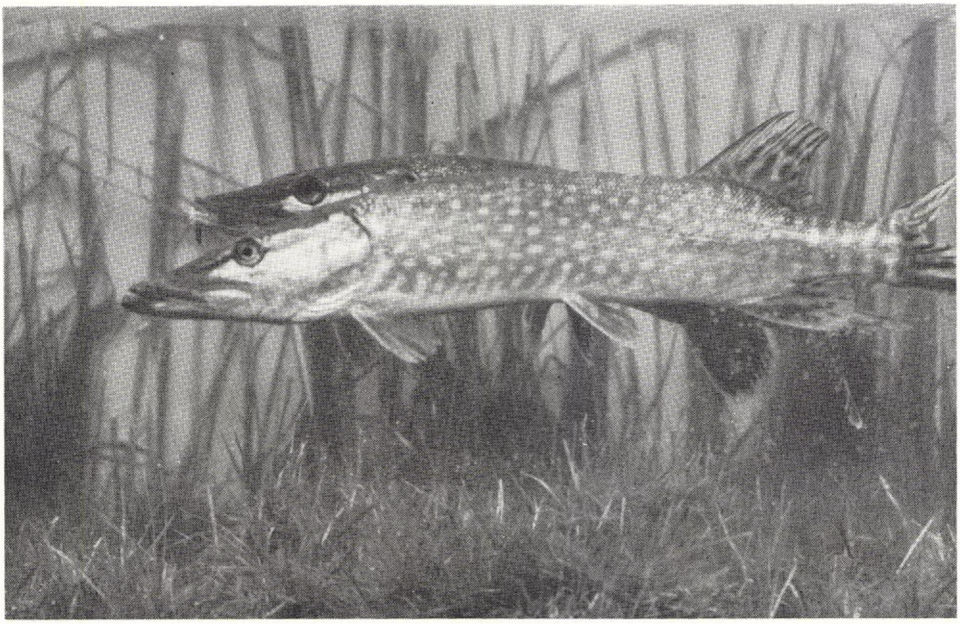

Fig. 6. The mixing stroke. The female is closest to the pane. The caudal part of the male's body sweeps forward under the vent of the female, where the eggs can be distinctly seen. The caudal fin of the male is visible under the anal fin of the female, and its anal fin, which is still bent towards the female, is seen behind the latter's genital opening. — Photogr.: K.-J. Gustafson.

The erection of the pelvic fins in the female marks the onset of the ejection of a portion of eggs. While the pelvics become erected, the ventral contour of the female's belly is curved downward, indicative of a pressure suddenly arising in the body cavity, and simultaneously a depression appears in the hypaxial part of the lateral musculature, in the area between the pectoral and pelvic fins. This depression rapidly becomes very marked. The frame of the film in which the pelvics have been turned back to their normal position after the erection shows it as a deep oval pit in the flank of the fish, extending from slightly behind the pectoral fins to the pelvic fins. In the following frames this depression then travels backward, disappearing finally on reaching the region just in front of the anal fin, where the genital opening is situated. The appearance and backward displacement of the muscular depression covered 5 to 7 frames of the film (Fig. 7 a—e).

3. While the muscular depression in the flank of the female moves backward, the male turns his head away from the female, and closes its mouth, while the bending of its genital region travels backward, causing a straightening of his body. The movement of the trunk of the male is then continued as an opposite bending during which its tail fin strikes towards the female.

Fig. 7. The female erects its pelvic fins, when hit by the mating thrust of the male (a). A deep depression appears in the hypaxial musculature of the female, and travels backwards to the region of the genital opening, indicating the ejection of a portion of eggs (b—e). These pictures are single frames from the ciné-film. — Photogr.: K.-J. Gustafson.

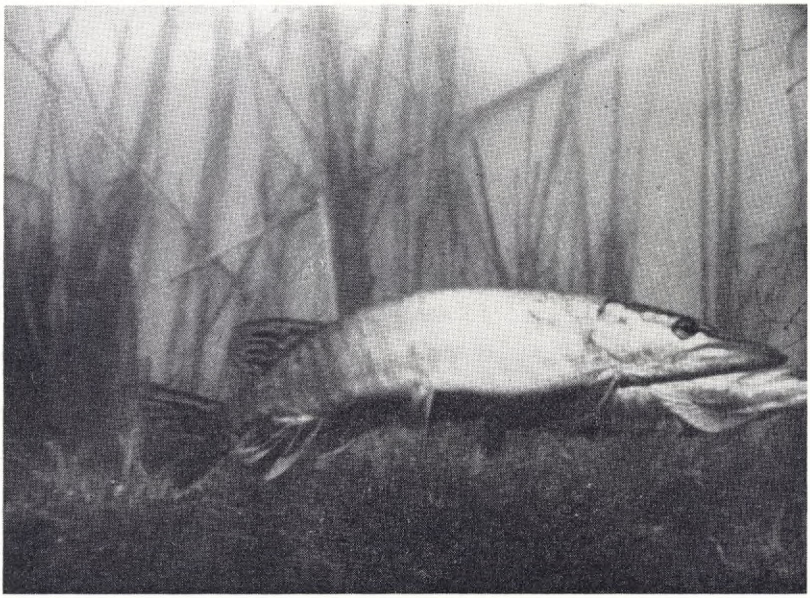

Fig. 7 a.

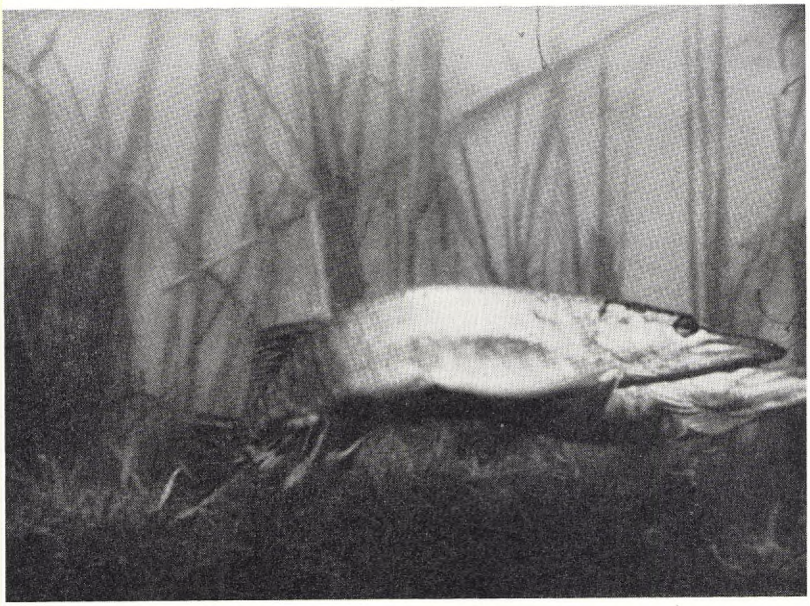

Fig. 7 b.

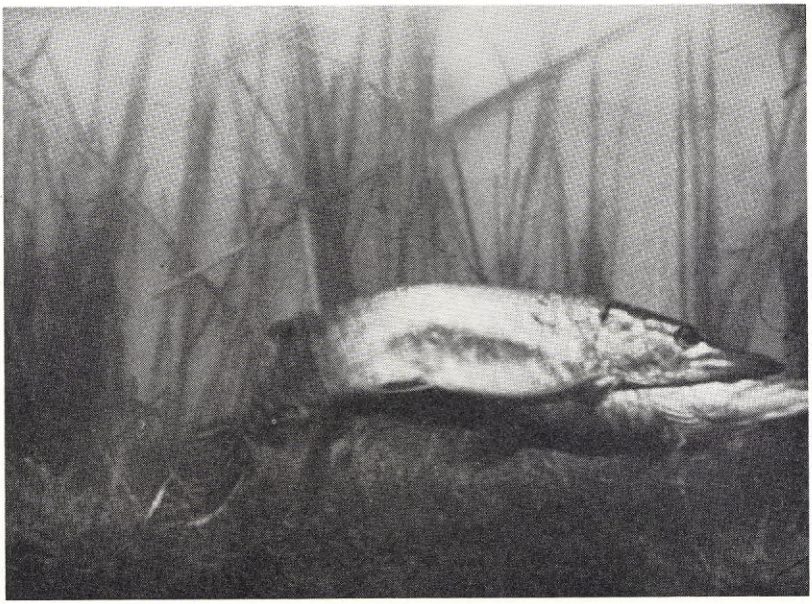

Fig. 7 c.

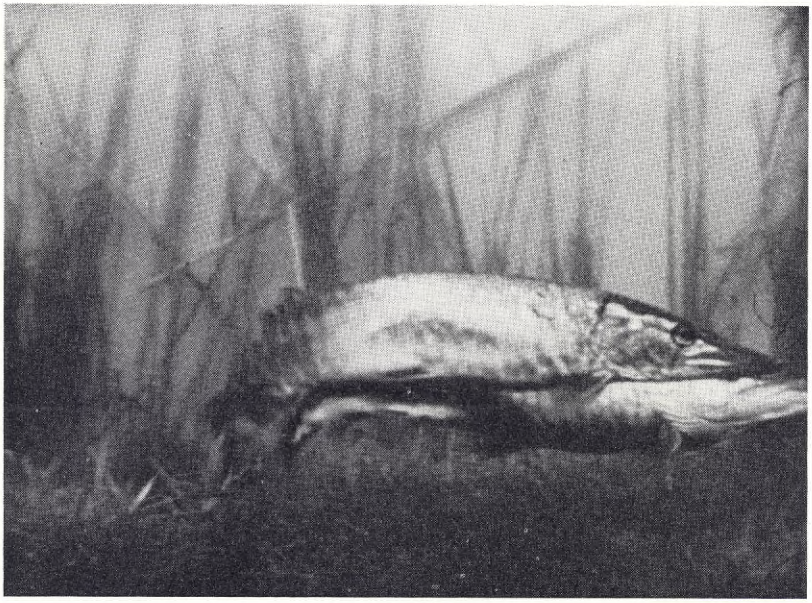

Fig. 7 d.

Fig. 7 e.

As the female has been thrown sidewards and upwards by the powerful mating thrust, it is usually not hit by this stroke. If the fish are not hampered by too dense vegetation, the tail fin of the male as a rule sweeps forward under the female, reaching the genital region of the latter at about the moment, when the muscular depression in its flank has just disappeared, and the shedding of a portion of eggs has been compleated. This final tail stroke of the male could be called the mixing flap (Fig. 6). The male then straightens its body, the erection of its paired fins disappears, and both fish regain their normal swimming posture. This third and last stage of the spawning act, from the mating thrust to the completion of the final straightening of the male's body, covered 10 to 15 frames of the film.

The sequence of movements described above was found in all the 15 slow motion records of the spawning act, and these records were made of several different pairs. In 4 of these records the female was closest to the front pane, allowing observations on the contractions of the lateral musculature, whereas in the 11 other records the male was next to the pane. All these movements, which compose the spawning act, contribute to bring the genital openings of male and female into close proximity of each other, to mix up the male and female sexual products, and to scatter the eggs. As mentioned, during the courtship swimming the genital opening of the male is usually ahead of that of the female. The forward stroke of the tail fin during the mating thrust results in a backward movement of the male, while the female swims forward during all stages of the spawning act. Consequently, the genital openings of the two fish move towards and past each other, and just at the moment they pass each other, the sideward bending performed by the male in the mating thrust brings them in very close proximity of each other. During the mating thrust, the anal fin of the male is folded towards the female, and is brought below the latter's vent like a spoon. It thereby probably contributes to direct the jet of sperm towards the genital opening of the female, and to prevent the eggs from sinking until they have met the sperm. This folding of the anal fin of the male is also maintained during the mixing flap. The dorsal fin of the male is not folded, nor the dorsal and ventral fins of the female.

The fact that the genital openings of male and female rapidly move past each other in opposite directions during the shedding of eggs and sperm apparently facilitates a thorough mixing of the sexual products, and also the subsequent mixing flap of the male's tail fin, by producing a jet of water, contributes to this stirring as well as to the scattering about of the eggs. Movements with a similar function occur in some other species of fish as well, for example in the burbot, *Lota vulgaris,* which also scatters its eggs about (FABRICIUS 1954 a).

8. Reactions to Some Environmental Stimuli During the Spawning

The water supplied to our tanks was pumped up from a depth of about 4 metres in Lake Mälaren, and was consequently considerably colder than the very shallow water at the actual spawning grounds close to the shoreline. On May 4th, for example, we measured a water temperature of +17°C at a place in the flooded meadows, where several groups of spawning pike were observed, while the temperature in our tanks was only +5.5°C. The pike used in our experiments had been caught in fyke nets in the shallowest parts of the spawning grounds, and the females had running roe, indicating that they had already begun their spawning.

From May 3rd to May 7th 10 females and 6 males were kept in the big tank in which the temperature rose slowly from +5.5° to +7.6°C. No spawning occurred however, except on May 5th, when some few series of spawning acts were observed in the afternoon, at a temperature of +7.5°C. Aggressive behaviour and courtship were occasionally observed every day, but the courtship did not proceed to spawning, and most of the time the pike were very inactive, resting on the bottom.

On May 8th electric heating elements were inserted into the tanks, and this enabled us to maintain the water temperature between +12.5° and +18.5°C from May 9th to May 12th, when the experiments were terminated. This high temperature had a striking effect on the behaviour of the pike. During this period intense spawning occurred every day, often by several couples or groups simultaneously, and most of the new pike introduced every day from the lake continued their spawning in the tanks, often already after a few hours. On May 8th, while the water temperature rose gradually from +7.6 to +12.5°C, some courting was observed, but no spawning occurred.

These aquarium experiments confirm the findings of several field observers, viz. that a warming up of the water stimulates the spawning of the pike, while a cooling down suppresses the spawning activity (Svärdson 1947, Clark 1950, Fabricius 1950, and others). As this phenomenon was, in the aquarium experiments, observed in pike which had already begun their spawning, the temperature is apparently not only a factor influencing the ripening of the gonads, but affects also the intensity of the spawning after this ripening has been compleated. This is also evident from the fact that at the natural spawning grounds the pike seek out the warmest places. Considerable temporary differences of temperature occur in the shallow water of the flooded meadows at Drottningholm. While water temperatures up to +17°C could be measured at sunny and calm places, e.g. in the shelter of groups of trees or high reeds, the temperature could, at the same time, be as low as +4° at other nearby places which for the moment were subjected to strong wind, or in the shadow of trees. Fyke nets were placed out in all parts of the spawning grounds, and it was obvious that the largest daily catches were made in the nets that had been in the warmest water, indicating a concentration of the spawners to the warm areas. Direct field observations gave the same result. Actual spawning occurred almost exclusively within the warm areas, but their location changed from day to day, according to the direction and strength of the wind, and even from hour to hour, depending on the position of the sun. This also demonstrates that during a field investigation measurements intended to illustrate the influence of temperature on the spawning should not be made at one point of the shore only.

At sunset the pike abandon the shallow spawning grounds, retreating to somewhat deeper water. In the spawning area at Drottningholm they probably spend the night in or just outside the belt of *Phragmites*-reed which forms the borderline between the flooded meadows and the open waters of the lake. One of the reasons for this abandoning of the spawning grounds in the evening is certainly the cooling down of the shallow water after sunset, but also the decreasing intensity of the light seems to be of importance.

In the experimental tanks, which received daylight from the windows of the aquarium building, the spawning also ceased at sunset, though no cooling down of the water occurred, the electric elements maintaining the water temperature at a fairly constant and comparatively high level even during the night. If, however, the artificial lights were switched on, the pike resumed spawning, but ceased this activity as soon as the lights were again switched off. In this way spawning could be induced at any time of the night, though with some difficulty around midnight, probably because at this time the spawning was suppressed by the inactivity period of the physiological diurnal rhythm, which is known to persist for some time even if the distribution of the light and dark periods is artificially altered.

Anyhow, these observations strongly support the view that light actually stimulates the spawning in the pike. It seems, however, probable that the influence of the light is, at least partly, an indirect one, i.e. that an intense light improves the visibility and brightness of visual stimuli emanating from the sexual partner and from the optimal bottom material. In passing it should be mentioned that the intense light of the ten 500 watt bulbs fitted over the photographing tank did not at all disturb the pike, but rather stimulated their spawning. This is not surprising as the pike often spawn in bright sunshine and in shallow water.

During the aquarium experiments some interesting observations were made on the reactions of the spawning pike to the vegetation and the bottom substrate. In the photographing tank the bottom of the foreground was covered by an even carpet of short grass, taken from a garden lawn, while a file of *Phragmites*-reed had been arranged in the background, along the rear wall (Figs. 1—6). During the courtship swimming and the spawning the pike made no attempts at penetrating into the spaces between the *Phragmites*-stems. They constantly kept above the lawn, at a distance of about 5 to

15 cms from its upper surface. They did not increase this distance if the water level of the tank was raised. Thus, by maintaining the depth of water at about 50 cms, we could induce the pike to spawn so far below the surface that no splashing occurred, and could thus save the hot photographing bulbs from bursting, which instantly takes place if they are hit by drops of water.

Similar observations were made in the big tank, where a mat of spruce-fir was used as spawning substrate. The spawning pike loced themselves above the mat of fir, about 5 to 15 cms from its upper surface, but did not enter the openings in the fir mat, nor did they swim in between some vertical branches which almost reached the surface of the water. Close observations showed that this orientation is due mainly to the movements of the female. During the courtship swimming, the female always turned on reaching the borderline between the mat of fir and the bare bottom of the rest of the tank, and the male followed, orientating itself to the head of the female. As a result of this behaviour almost all the eggs were deposited within the mat of fir.

The female thus determines the place of spawning. This is not very common in fish but has, in addition to the pike, been shown in some other species, for example in *Umbra lacustris* (GEYER 1940), in *Fundulus notatus* (CARRANZA and WINN 1954), and in the nest-digging species of *Salmonidae* (JONES and KING 1949, JONES and BALL 1954, FABRICIUS and GUSTAFSON 1954). The intense eye movements of the female pike during the courtship swimming indicate that her orientation in relation to the bottom substrate is probably based mainly upon visual cues, like the orientation of the female char to the gravel, which has been shown to be based on visual stimuli (FABRICIUS and GUSTAFSON 1954).

Apparently, the optimal spawning bottom for the pike is a dense mat of short vegetation, and the spawners try to reach and maintain a position above this mat, and at some distance from its upper surface. This is the reason, why spawning pike in very shallow water ascend so high that their backs become visible above the surface, instead of penetrating down into the vegetation. The type of vegetation that forms the mat seems to be of very small importance. The pike is known to spawn in vegetation of several different types (FABRICIUS 1950), and even on bottoms of soft silt, filled with a layer of decaying vegetation (CLARK 1950). Some control experiments showed that, in the absence of vegetation in an aquarium tank, the pike finally spawn even above a smooth bottom of sand or gravel.

Field observations on the spawning of the pike in Lake Vojmsjö in Swedish Lapland led FABRICIUS (1950) to the assumption that the water temperature and the sight of vegetation cooperate in releasing the spawning activity in this species, and this seems to have been fully confirmed by our aquarium experiments. Spawning was induced by a high water temperature as well as by the presence of a special type of vegetation, and, evidently, the reaction to this vegetation was, at least in part, based upon visual stimuli.

9. Discussion

As has been shown by MONTÉN (1948), the pike fry after hatching move towards the densest vegetation. There, by means of the sticky secretion of some areas of the head, they attach themselves to plants and debris, preferably close to the water surface. During the early stages of their life the young pike then remain in the belt of dense vegetation in the shallow water close to the shoreline, and particularly in flooded meadows, where the food supply is rich, and they find shelter from enemies. Outside this belt of dense vegetation young pike fry would hardly survive.

The positive reactions of the spawning pike to warm water and to the sight of carpets of grass or other plants automatically takes them to the vegetation belt of the shallow water, thus securing the deposition of the eggs within the optimal habitat of the young. As the young pike are not very mobile, a too dense seeding of the very numerous eggs of a female would lead to severe competition for food among the young, resulting in a low growth rate and a high mortality. A too dense grouping of the eggs would certainly also increase the damage done by predators. For these reasons it seems obvious that an even scattering of the eggs within large areas of the rather uniform but comparatively narrow belt of dense vegetation is advantageous. This even distribution of the eggs is secured by the constant forward swimming during the spawning as well as by the maintainance of a position above the carpet of vegetation, and by the specialized movements of the spawning act.

As a restriction of the spawning activities to a territory would counteract the spreading out of the eggs, also the lack of territorial behaviour in the pike must probably be regarded as an adaptation to the necessity of scattering the eggs over wide areas. Furthermore, the complete lack of special spawning markings in the pike apparently is a consequence of the lack of territorial behaviour, one of the most important functions of the conspicuous markings which appear in animals at the onset of the reproductive period being to act as signals releasing aggressive behaviour in the territory owners, and flight or submissive behaviour in trespassers upon the territories (cf. TINBERGEN 1948, and others). It was pointed out by NOBLE (1938) that there often exists a correlation between territorial behaviour and the occurrence of a particular nuptial coloration, and this correlation has in some cases made it possible to predict, whether territorial behaviour will be found in a certain species of fish or not. As the char has very conspicuous nuptial markings, it was thus predicted that it would have a territorial behaviour (FABRICIUS 1950, p. 92), and this was fully confirmed by aquarium experiments (FABRICIUS 1953, FABRICIUS and GUSTAFSON 1954). On the other hand, it was predicted that there would be no territorial behaviour in the pike, which completely lacks nuptial markings (FABRICIUS 1955, p. 57), and the aquarium experiments described in the present paper have corroborated also this prediction. Within the family *Esocidae* conspicuous spawning markings are known only in the genus *Umbra,* and in this genus there exists also territorial behaviour, and the eggs are guarded in a nest (GEYER 1940).

It has been pointed out by TINBERGEN (1952 b) that the effect of spacing out, reducing the competition for food and the damage done by predators, is an important function of the territorial behaviour of many species of birds, and there is no doubt that this is also one of the main functions of territorial behaviour in fish (cf. TINBERGEN 1953, FABRICIUS 1953). At the first glance it might seem paradoxical that this is also the effect or "function" of the lack of territorial behaviour in the pike. Obviously a spacing out of the eggs is for many reasons necessary for most species of fish, and this can be attained by movements of the spawning fish over wide areas, as in the pike. Yet such movements are not possible in species which for their reproduction are dependent on structures or objects which, like a patch of suitable gravel for the char or a mussel for the bitterling, do not form continuous surfaces which cover large areas. In such species a territorial behaviour is necessary for securing the spacing out of the offspring, by spacing out the spawning sites of the different couples. This fully agrees with the statement by TINBERGEN (1953) that reproductive fighting occurs mainly in species of animals which for their reproduction depend on objects or structures which can not be shared by too many individuals.

In fish also the number of eggs seems to be adapted to these circumstances. As a rule the number of eggs in relation to the size of the female is smaller in territorial species than in non-territorial ones. This is understandable, as in the former category the eggs of each female are deposited within a restricted territory, where a concentration of too many eggs would be disadvantageous, while in the latter category, where each female distributes its eggs over a wide area, there must be a strong selection in favour of a high number of eggs. As has been shown by SVÄRDSON (1945), LINDROTH (1946) and others, the number of eggs is very large in the pike.

These differences can be clearly demonstrated, for example, in the family *Salmonidae* by comparing the non-territorial genus *Coregonus* with the territorial genera *Salmo, Salvelinus,* and *Oncorhynchus.* As an example, a female whitefish with a body length of 30 cms has about 5,700 eggs (TOOTS 1951), while a female char of the same size has only about 800 eggs (MÄÄR 1949). SVÄRDSON (1949 b) has discussed some other selective factors responsible for reduced eggs numbers. He did not, however, consider this correlation between territorial behaviour and egg number, but formulated a hypothesis according to which the most important of the selective forces working for reducing the egg numbers would be a premium for large and consequently few eggs. These would give rise to large larvae which would gain in the competition with the smaller larvae of females with smaller but more numerous eggs.

The aggressive behaviour, shown occasionally by the male pike, is not restricted to a territory, but is much intensified in the presence of a ripe female. It might thus serve as counteracting a concentration of too many males around a female, what would lead to a waste of germ cells (TINBERGEN 1953). It should, however, be mentioned that the pike do show aggressive behaviour even when no specimens of the opposite sex are present, and this behaviour certainly also contributes to a spacing out of the fish over the spawning grounds. A similar aggressiveness, which is not restricted to a territory, occurs in several genera of the family *Cyprinidontidae,* for example in *Xiphophorus* (BRADDOCK 1945, 1949, SCHLOSBERG, DUNCAN and DAITCH 1946) and *Lebistes* (BAERENDS, BROUWER and WATERBOLK 1955).

As has already been mentioned, all the movements included in the spawning act of the pike apparently contribute to the fertilization and scattering of the eggs. The perfect synchronization of the movements of the male and the female is remarkable, considering the short duration of the spawning act which, to judge from the analysis of the slow-motion records, lasts only between 0.5 and 0.8 seconds, from the onset of the lowering of the branchiostegal membrane to the completion of the straightening of the male's body after the mixing flap. This synchronization is obviously secured by a system of signals. During the courtship swimming the level of stimulation approaches the threshold necessary for the release of the spawning activities in the female, and reaches this threshold in the male. The sequence of motor patterns which are thus released in the male includes a number of movements, apparently acting as signals. These are sufficient to provide the small amount of further stimulation which is still required for bringing the level of stimulation above the threshold for release also in the female. These signals include visual stimuli, such as the lowering of the branchiostegal membrane and the opening of the mouth as well as tactile stimuli, such as the introductory tail flap and the mating thrust. All these stimuli probably support each other in a cumulative way, resulting in a release of the ejaculatory movements of the female approximately at the moment of the mating thrust. Possibly also chemical stimuli might be involved. MC NAMARA (1937) supposes that the sense of smell plays a part in the sexual behaviour of the pike, because he observed a female swimming over the spawning ground, followed a few minutes later by a male along the same route that she had taken.

The male pike seem to prefere females which are larger than themselves. As has been shown for *Lebistes* by BAERENDS, BROUWER and WATERBOLK (1955), the size of the female seems thus to be one of the stimuli which release the sexual behaviour of the male. In the pike this apparently is an adaptation to the specialized spawning movements, since the movements contributing to the mixing up of the sexual products and the scattering of the eggs function properly only if the genital opening of the male is ahead of that of the female at the onset of the spawning act. And since the male orientates itself in relation to the eye region of the female, this mutual position of the genital openings is reached only, if the male is smaller than the female.

The ejaculatory mechanism in the pike would deserve a special investigation. Circular as well as longitudinal muscles are present in the wall of the ovary (cf. for example, GASCHOTT 1928), and contractions of this musculature certainly contribute to the ejaculation of the eggs. By diminishing the volume of the ovaries, which would result in a reduction of the pressure in the body cavity, such contractions could also be responsible for the appearance of the depressions in the body wall of the female during the shedding of the eggs. The backward travelling of these depressions indicates, however, that they must also be due, at least in part, to contractions of the hypaxial musculature of the body wall. Other evidence in favour of this view has been gained by observations on the spawning behaviour of salmonids. In female char we have noted similar depressions in the body wall during the shedding of the eggs, though the ripe eggs of the salmonids are known to float freely in the body cavity, where they are not surrounded by the walls of the ovaries, but only by the body wall and its musculature.

The slow-motion pictures did not show any depressions in the body wall of the male pike during the spawning act. It should, however, be mentioned, that the details of the male were not very sharp in the pictures showing the mating thrust, the movements of the male being extremely rapid, some parts of its body always being, more or less, out of focus as a consequence of the sharp S-bend of its body. Moreover, the possibly existing depression in the body wall of the male can not be very conspicuous, since the amount of sperm emitted at each mating act is so small that it can be seen only with great difficulty. It has been presumed by LINDROTH (1946) that during the spawning act the male pike ejects an amount of urine from its bladder, and that this jet of fluid carries a small amount of sperm out of the testes. The ejaculte should thus be a diluted mixture of sperm in urine. According to LINDROTH the ejaculatory apparatus of the male pike should thus work in a manner like a squirt bottle, where the jet of air from the rubber ball carries an amount of finely distributed fluid out of the bottle. This hypothesis has, however, to be tested experimentally, for example by watching the spawning of male pike into the urinary bladder of which some coloured fluid has been injected.

There is good evidence that many of the specialized movements included in the reproductive behaviour of fish have been derived from swimming movements. This has been shown for several species of *Salmonidae* by FABRICIUS and GUSTAFSON (1955), and for *Blennius* by WICKLER (1957). In the pike the derivation of the spawning activities from swimming movements seems to be beyound any doubt. Most of the spawning activities consist of different bendings or undulations of the body which appear as only slightly modified swimming movements, and which still have a locomotory function in addition to more special functions, such as bringing the genital openings of the two fish close to each other, or scattering the eggs. The movements of the male pike during the spawning act can be considered as a forward swimming which suddenly changes into a backward swimming, and in which some of the movements have become "exaggerated" and specialized to serve the bringing together of the sexual products and the scattering of the eggs. The change in the direction of swimming could probably be a result of a sudden shifting of the orientation of the male from the eye region of the female to the region of her genital opening at the onset of the orgasm. Such a change in the orientation of the male would lead to a backward movement, since the genital opening of the male is ahead of that of the female during the courtship swimming.

In connection with the bendings of the body during the spawning act it should be mentioned that the introductory tail flap of the male pike is very similar to the movement known as "tail beating" which occurs in the fighting pattern of cichlids (SEITZ 1940, BAERENDS and BAERENDS 1950) and some other fish, for example *Rasbora* (WICKLER 1954), *Tanichthys* (FABRICIUS 1954 b), and *Blennius* (WICKLER 1957). In the pike, however, we have not seen this movement in aggressive encounters.

Apart from the activities derived from swimming movements, the spawning act of the pike includes some movements which probably have developed from displacement activities or from incipient movements belonging to drives other than the sexual drive. This seems to be true especially in the case of the opening of the mouth of the male at the onset of the mating thrust. The male opens its mouth at the moment of turning its head towards the female, thus suddenly facing the head of the latter just in front of its own nose by both its eyes, and to the naked eye this opening of the mouth appears as a rapid snapping. As it is known that the posture in which an animal finds itself, when a displacement activity is likely to occur, often decides which activity will be used as an outlet (TINBERGEN 1952), it seems probable that the opening of the mouth at the moment of the male suddenly facing the head of the female originates from a displacement biting, or perhaps from an incipient biting. This view seems to be supported by an observation which indicates that the biting drive might sometimes really be activated during the spawning. We thus observed one single case in which the male attacked the female, and repeatedly bit it in the flank immediately after a series of spawning acts. The probable origin of the mouth-opening in the orgasm of the male pike from displacement biting or from incipient biting might be of some interest, as the origin of the very conspicuous opening of the mouth, which is so characteristic of the spawning behaviour of the *Salmonidae,* is not so clear, perhaps because it has become more ritualized. The lowering of the branchiostegal membrane, the opening of the mouth, and the erection of the paired fins are elements which the sexual behaviour of the male has in common with the aggressive behaviour, within which they occur in the threat posture. As has been pointed out by TINBERGEN (1951, 1952 a) it is very common in animals that the aggressive and the sexual behaviour share a number of motor patterns.

As has been mentioned in Chapter 3, the repulsive headshaking in the female pike could have developed from the movements of adjusting a caught prey into a position suitable for swallowing. There exist, however, also other possibilities. The repulsive headshaking is very similar to the sideway swing of the head by which some cichlids elicit the following response of their young. According to LORENZ (1950) this signal movement has probably been derived from incipient swimming movements. This could be the case with the repulsive headshaking as well, particularly as the unripe female pike tends to swim away from the male in the situations in which the shaking of the head occurs.

From the point of view of comparative ethology it is remarkable that the spawning behaviour of the pike shows very great similarities to that of cyprinidontid fish belonging to the genus *Fundulus.* According to the detailed description of the spawning behaviour of *Fundulus notatus* by CARRANZA and WINN (1954) the body of the male is bent during the spawning act in an S-shape, while the body of the female is bent in a J-shape, and the sexual products are emitted at a sideward flap by the male against the female, just as in the pike. Moreover, the anal fin of the male is, as in the pike, folded towards the female, but different from the pike, also the dorsal fin is folded in this way. The mating thrust of the male pike has also rather great similarities to the copulatory thrust of the males of the viviparous genera of *Cyprinidontidae,* which has been described, for example, by CLARK and ARONSON (1951), CLARK, ARONSON and GORDON (1954) and by BAERENDS, BROUWER and WATERBOLK (1955), and a bending of the body in an S-shape occurs in the sexual display of the males of these cyprinodontids.

Some genera of *Cyprinodontidae,* as for example *Fundulus, Epiplatys,* and *Belonesox,* show great superficial similarities to the pike in their general appearance as well as in their feeding behaviour, and some earlier authors regarded the *Cyprinodontidae* and the *Esocidae* as more or less closely related. The *Esocidae, Umbridae,* and *Cyprinodontidae* were thus grouped together under the name *Cyprinodontoidea* by GILL (1872), and BOULENGER (1904) included the *Esocidae* and the *Cyprinodontidae* in his suborder *Haplomi.* This view has, however, been abandoned by modern fish taxonomists. The *Esocidae* are thus placed within the suborder *Esocoidei* of the order *Clupeiformes* by BERG (1947), while the *Cyprinodontidae* are put into the suborder *Cyprinidontoidei* of another order, the *Cyprinodontiformes.* The great similarities in the spawning behaviour of *Esox* and *Fundulus* would thus supply a remarkable example of convergent evolution in two groups between which there are no close phyletic relations.

10. Summary

The spawning of the pike was watched in the field as well as in big aquarium tanks, and the movements were recorded on ciné-film, partly in slow-motion.

The pike do not maintain spawning territories, but aggressive behaviour often occurs, when two individuals meet within the spawning grounds. In most cases this aggressiveness is limited to a threat posture in which the branchiostegal membrane is lowered, the back arched, the paired fins expanded to a maximum and the mouth slightly opened. One case of real attack was observed in which a male bit an opponent in the flank.

Unripe females adopt the threat posture on the approach of a courting male, or show the male off by a sudden sideward bending of the head. Ripe females respond to the approach of a male by a slow forward swimming which initiates the courtship swimming of the couple. The males seem to prefer females which are larger than themselves. During the courtship the two fish slowly swim side by side, orientating themselves so that the eye region of the male is on a level with the eye region of the female. As a result of this orientation and of the different size of the partners, the genital opening of the male is during the courtship swimming usually slightly ahead of that of the female.

To the naked eye the spawning act appears as a sudden flap of the male against the female. Such spawning acts, repeated with short intervals, form long series, separated by periods of rest. During the spawning the pike swim forward, mostly parallel with, and close to the shore. Each female is usually followed by two or three males, but in small tanks one male becomes dominant, preventing the other males from taking part in the spawning. Some cases of homosexual behaviour have been observed in males.

The slow-motion pictures were used for an analysis of the spawning act, its total duration being only about 0.5 to 0.8 seconds. While the two fish swim side by side, the male at first lowers its branchiostegal membrane, and then performs an introductory flap by its tail fin against the female. After the introductory flap the tail fin of the male is moved to the opposite side in a powerful braking stroke. This results in a backward movement of the body of the male, so that his genital opening passes that of the female. The braking effect is supported by an erection of the paired fins. Simultaneously the male bends the region of his genital opening towards the female, hitting it by the mating thrust, which is so powerful, that the female is flung sideward and upward. When hit by the mating thrust of the male, by muscular contractions the female sheds a portion of eggs. These contractions are visible as a backward travelling depression in the hypaxial musculature of its body wall. At this stage the body of the female is bent in a J-shape, with the tail part towards the male, while the body of the male forms an S, with the head to-

wards, and the tail pointing away from the female. The male opens its mouth, when bending his head towards the female. After the mating thrust, the tail fin of the male is moved towards the female, striking forward under the latter's belly, and causing a thorough mixing of the sexual products and a scattering of the eggs.

The spawning of the pike is stimulated by high water temperature and by intense light. During the spawning the female, apparently mainly by a visual orientation, tries to reach and maintain a position above dense but comparatively short vegetation over which the eggs are sprinkled. This behaviour secures the deposition of the eggs within the optimal habitat of the young, and the specialized movements of the spawning act contribute to the scattering of the eggs.

The absence in the pike of special spawning markings is a consequence of the lack of a territorial behaviour. This is missing, as it would counteract the spacing out of the eggs of each female. Another consequence of the lack of territorial behaviour is the high number of eggs in the female pike. As a rule females of territorial species have a comparatively small number of eggs.

Most of the movements included in the spawning act of the pike have probably been derived from swimming movements, but the repulsive head-shaking of the female and the opening of the mouth in the male seem to originate from displacement activities, or from incipient movements belonging to drives other than the sexual drive.

There is a discussion on some striking similarities between the spawning behaviour of the pike and that of the cyprinodontids, and particularly of *Fundulus*.

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Observations in a Stream Tank of Territoriality and Competition in Juvenile Salmon and Trout (*Salmo salar* L. and *S. trutta* L.)

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Contents

I. Introduction

For an increasing number of animal species it is demonstrated that the individual moves only within a very limited portion of the biotope. Consequently in these species the population can not be considered as a homogeneous, freely mixing group. Hediger (1946) stresses that the individual is fitted into a frequently narrow "Raum-Zeit-System" (space-time-system). In Anglo-Saxon literature the area over which the animal normally travels (Hayne 1949, Gerking 1953) is termed home range (Burt 1943). This conception was introduced, since in the field it was usually found difficult to decide whether or not the observer was faced with real territoriality. According to the universally accepted definition of territories given by Noble

(1939) these are defended areas, implying that the aggressive behaviour of the animal has to be directly observed.

For a great number of fishes in the sea, in lakes, and in running water field observations have proved the occurrence of restricted home ranges. For a general review the reader is referred to GERKING (1953). Anglers know very well that certain salmonids are remarkably stationary in running water, and this circumstance has also been mentioned at an early date by some biologists connected with pisciculture.[1] Only lately, however, has the stationariness been proved by real investigations, e.g. in *Salvelinus fontinalis* (SHETTER 1937), *Salmo trutta* (SCHUCK 1943, ALLEN 1951), *S. clarki* (MILLER 1957), and *S. salar* juv. (CARLIN, personal communication).

Up to recent years it was possible in the case of fishes to identify the territories in general with the spawning territories which latter had been made the subject of intensive investigation. THORPE (1956) writes: "Area defence by fish in a non-reproductive state may, for all we yet know, be quite exceptional". It seems difficult to argue against this statement, as the number of species in fish amounts to about 20,000, and as up to now non-reproductive territories have been demonstrated in considerably less than 100 species. In the course of the ten years which have passed, since GREENBERG (1947) demonstrated territoriality in the immature green sunfish, *Lepomis cyanellus,* it has, however, become increasingly evident that in many fishes this behaviour is an every-day phenomenon of the greatest importance for the understanding of the ecology of the species. So far such territories are known especially for fishes in running water (Centrarchidae, Salmonidae), but they have been shown, particularly by the investigations by KIRCHSHOFER (1954) of *Serranus scriba,* to occur also in marine fishes (cf. also BOPP 1957, p. 249, about *Gobius paganellus* and *G. niger*).

With salmonids in running water territories seem to be almost the rule. The list comprises a number of species, even if greatest care is taken to include only those in which area defence has been directly observed: *Oncorhynchus kisutch* (HOAR 1951), *Salmo trutta* (FABRICIUS 1953 b, STUART 1953), *S. salar* (LINDROTH 1956), *S. gairdneri* (FABRICIUS 1955, STRINGER and HOAR 1955, NEWMAN 1956), and *Salvelinus fontinalis* (FABRICIUS 1955, NEWMAN 1956).

This paper is not the result of a well planned investigation. The numerous hours, spent in front of the panes of the aquaria were distributed over the years 1954—1957, when these observations were carried out side by side with other studies. Experiments could be arranged for only on a much smaller scale than desirable.

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[1] E.g. NORBÄCK (1884): "No fish remains for such a long time on its station without moving from there as the river trout . . ." (Transl. from the Swedish).

II. The Stream Tank and the Experimental Fishes

The major part of the observations which form the base of this paper have been carried out in the large stream tank at the Salmon Research Laboratory. The laboratory is situated at the river Indalsälven in the easternmost corner of the county of Jämtland (62°57′N). For a complete description of the aquarium the reader is referred to LINDROTH (1954).

In order to make possible observations also at great turbidity of the water the aquarium was divided by a longitudinal wooden partition. Thereby the bottom surface was reduced to less than one half, and measured 85 by 950 cms.

The bottom was covered to a thickness of about 30 cms. with coarse gravel and stones measuring up to 10 cms. in diameter. The surface has been levelled as much as possible, care being taken to produce the greatest uniformity all over the aquarium. Of the bottom a photographic map was produced which proved entirely indispensable for the study of the movements of the fishes in the aquarium.

Normally the level of the water was kept between 20 and 30 cms. above the surface of the gravel. According to determinations by means of an OTT-propeller the maximum velocity of the current was displaced slightly towards the posterior longitudinal wall of the aquarium. This lack of symmetry appeared, however, not large enough to influence the distribution of the fishes in the aquarium. The velocity of the current was as a rule determined by taking the time with just floating ping-pong balls, which had to the greatest extent been filled with water, or with tubes of organic glass weighted so as to float in a vertical position. In the cases when the determination has been carried out of the last-mentioned method the velocity of the current is given, e.g. as the average velocity in the uppermost 10 cms. of the water, implying the use of a tube which reached down to this depth. The velocity of the current was a rule kept between 18 and 25 cms./sec. Occasional larger variations could not be avoided during the part of the summer, when timber was floated down the river, and great quantities of refuse of the logs quickly clogged the gratings. On the occasions, when special experiments demanded as constant velocity of the current as possible, the grating had to be brushed clean at frequent intervals.

Through skylights the daylight has access to the aquarium. During the course of the day different parts of the bottom receive a very varying illumination. A narrow strip along the posterior longitudinal wall was in shadow for the greater part of the day. Even these great differences in the illumination did not seem to cause any disorder apart from the fact that occasionally the fish, on being disturbed, fled into the shadow.

The temperature of the water of the river only seldom rose above 17°C.

The aquarium contained a fairly rich bottom fauna recruited from the drift with the water of the river. The composition of the fauna obviously varied with the seasons, but as a rule the majority of the groups of insects which are characteristic for running water, particularly *Trichoptera, Ephemerida,* and *Plecoptera,* were represented.

Macroscopic vegetation was on the whole missing, but a few stones could be covered with *Ulothrix,* and tufts of *Batrachospermum* occurred here and there.

On account of the rich supply of natural food the fishes grew normally without artificial feeding, provided that the aquarium was kept moderately stocked.

Juvenile salmon upon different stages of development and trout fry were obtained from the breeding station connected with the laboratory. Trout parr and also a smaller number of salmon parr were caught in a brook near the laboratory.

Before the transfer of the fish into the aquarium it was found suitable to lower the velocity of the current to about 15 cms./sec. In spite of this measure newly transferred fish, both bred and wild, seemed to find difficulties with the current. Immediately after the transfer the fish drifted or swam downstream until arrested by the outlet grating. There they stood, and fought against the current at all depths, close to the grating. Unless the velocity of the current was lowered before the transfer, it could frequently happen that one or several of the fish could not resist the current, but were pressed against the grating, and succumbed.

The transferred fishes recovered, however, quickly. Already in the course of the next few hours the first signs of aggressiveness appeared, usually in the individuals which stayed closest to the bottom. After this the process could be speeded up by a raising of the velocity of the current which could be carried even above normal. This pressed the fishes towards the bottom, and their aggressiveness increased. This in turn resulted in a gradual spreading up-stream in the aquarium, the fishes moving close to the bottom. Within a short time the first, still not quite settled territories could be observed. This initial phase with great movability and constant aggressive contacts supplied rich occasions for the observation of e.g. the different types of threat displays. Frequently a short lapse of time resulted in more observations than an uninterrupted watch of many hours after the stabilization of the territories.

III. The Structure of the Territory

A. *Definitions*

"Territory is any defended area" (NOBLE 1939).

By territorial mosaic is meant a pattern of mutually adjacent territories. BAERENDS and BAERENDS (1950) use in the same sense the term "territorial society". In doing so they point out that the mutual aggressiveness towards each other does not with necessity exclude a simultaneous attraction between the individuals (cf. the colonies of gulls). In strictly territorial fishes such a "keeping together on the basis of reacting to each other" (TINBERGEN 1953) has, however, not yet been established. The aggregations occurring among them can just as well be explained as the result of stimuli within the abiotic environment (e.g. edaphic or hydrological factors), and in this case the term territorial association (corresponding to "association" in ALLEE 1931) could be applied. The term territorial mosaic simply indicates a structure, but implies nothing about the forces which hold the pattern together. For this reason the term is applicable also to the aggregation occurring amoung fry as the result of a still incomplete dispersal from the place of hatching.

Station (FABRICIUS and GUSTAFSON 1955; syn. "preferred station", HINDE 1952; "Heim erster Ordnung", HEDIGER 1946) is the place in which the occupant of the territory mainly stays, and where it also displays the maximum of aggressiveness.

B. *The Station*

The territorial conditions of the juvenile salmon and brown trout are characterized in a high degree by the fact that each individual possesses within its territory one strongly dominating, strictly localized station. There the fish spends the greater part of its time, from there it defends its territory, and this is the starting point for its feeding excursions.

In the aquarium the stations were always chosen in direct connection with a solid surface, i.e. the bottom or sometimes one of the walls of the aquarium. At normal velocities of the water (higher than about 15 cms./sec.) no permanent stations existed in the aquarium in really open water, more than a few centimetres from a solid surface. Changes of the velocity of the water brought about characteristic vertical displacements of the stations which were exposed upon the upper surfaces of the stones at feeble velocities, but transferred to increasingly sheltered place, when the current grew faster. A similar depression of the stations was observed in the aquarium also if the density of the population rose. This effect dropped if at the same time the turbidity of the water increased (flood in the river).

The special feeding technique of the juvenile salmon and trout (p. 69) probably brings about a primary demand for the best possible outlook from the station. Observations in the aquarium indicate that in the practical choice of the stations this demand must be renounced to, when the velocity of the current is fairly high. Besides, the competition for space can compel the fishes to choose sheltered stations also at moderate current. The turbidity of the water creates visual isolation of the individuals, and thus limits the pos-

Fig. 1. Salmon parr (fork length 58 mm.) in typical position at the station. Note, how the cranial edge of the pectoral fin is applied to the surface of the stone, while the caudal edge is twisted upwards.

sibilities of the aggressiveness from manifesting itself as competition within the population.

At the stations fry and small parr were seldom seen to swim against the current. The fish usually lay upon the substratum, facing the current. Upon a smooth surface the pectoral fins were in this case held laterally extended and twisted so that their cranial edge was applied to the substratum, while the caudal edge was directed obliquely upwards (Fig. 1). Owing to this hydrodynamically correct position small salmon parr were able without swimming movements to maintain themselves upon their stations in surprisingly swift current.

Larger parr of salmon and trout, however, frequently kept their stations while swimming against the current. Very often the fish, in doing so, occupied an almost fixed position, e.g. with the point of the nose some millimetres above the top of a certain stone. At stronger current it could easily be seen that the optical axes of the eyes of the fish retained a constant direction, while the body oscillated in the eddies. This produced the peculiar impression of the fish being suspended in the current with the eyeballs acting as universal joints.

The localization of the stations in the aquarium was remarkably constant.

In most cases their position could be indicated within a limit of a few millimetres. It was constantly observed, how the fish after each return from a feeding excursion by means of small adjusting movements took up exactly the same position with regard to the substratum.

In spite of the fact that the station as described here plays a quite dominating rôle as centre of the activity of the fish inside the territory, certain observations indicate nevertheless the possibility of the occurrence of secondary centres ("Heime zweiter Ordnung", HEDIGER 1946). Thus in August and September of 1955 I repeatedly observed an about 15 cms. long trout in a brook near the laboratory. There the brook is hardly 3 ms. wide, and the trout had its station almost in the middle of the current at a depth of about 25 centimetres. With the aid of polarizing spectacles and binocular the fish was easily identified. Every time the fish was frightened it turned with extreme swiftness — always taking a right turn —, and disappeared below a certain spot of the overhanging bank. The same spot was invariably resorted to, irrespective from which bank I approached.

Similar observations have in some cases been made in the aquarium, where larger parr of salmon and trout defended territories extending across the entire width of the aquarium. During at least two weeks in July 1955 a smolt of salmon had a well defined place of refuge at a somewhat projecting board in the rear wall of the aquarium.

When a larger parr of salmon or trout swam along the bottom, fry defending territories in the aquarium slid one by one down from their stations, and took shelter among the stones. The reaction functioned so well that fry could for several days occupy territories ("partial territories", GREENBERG 1947) within the territory of a larger fish. It was, however, not possible to ascertain that the fry made use of fixed places of retreat.

LINDROTH (1956) describes, how fry in the aquarium during the night "go to rest on the bottom — probably *in* the bottom as well". It could now be established that at least some fry with stations near the glass wall of the aquarium night after night made use of the same sleeping places in fissures between stones, at distances of at most a few centimetres from their stations.

C. *Boundaries and size of the territory*

From the station as centre the fish defends its territory. According to the definition the extent of the individual territory can be ascertained only by directly observing within what area an intruder is met by the aggressiveness of the occupant of the territory. An investigation of this kind was carried out on a small scale in July 1956, when the aquarium contained salmon fry of about 40 mms'. length. Fig. 2 accounts for the location of the aggressive contacts observed during an accumulated time of observation of 212 minutes.

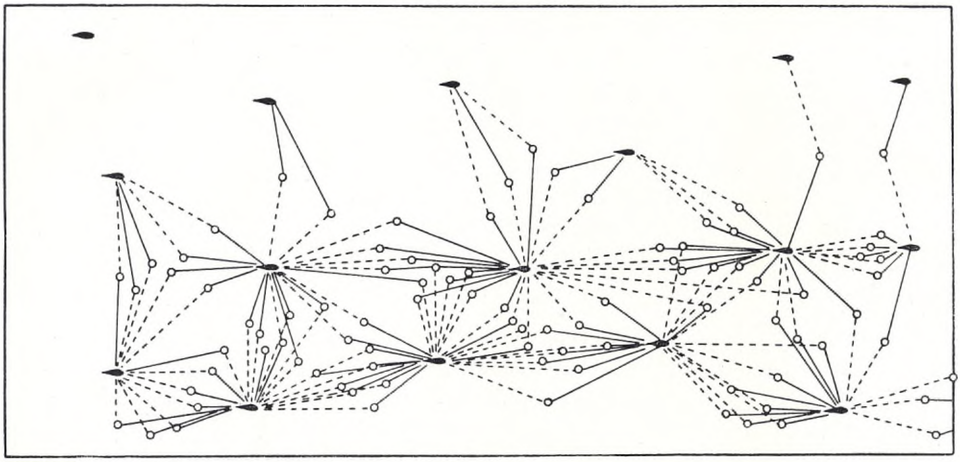

Fig. 2. Location of observed aggressive contacts within the territorial mosaic depicted in Fig. 4 a. Each circle shows the position of the intruder at the time when the defender first displayed aggressiveness. Unbroken and broken lines show direction towards intruding and defending fry, respectively.

Each dot in the figure indicates the spot occupied by the intruder at the moment, when the first signs of aggressiveness on the part of the defender were noticed. The spreading of the dots shows that the boundaries of the territories were by no means sharp. The wide "borderland" between the stations within which most of the conflicts took place, could be reduced to artificial bordering lines only by means of statistical treatment. For such a treatment my material is, however, too small.

The clearest idea about the nature of the boundaries of the territories is obtained by dummy experiments in the course of which the aggressiveness of the fish defending its territory is tested by confrontation with an "intruder". In an experiment with salmon fry on July 26—29, 1956 the dummy was a salmon fry of about the same size as the tested fishes (about 43 mms.). This fry had been fixed in formol in lateral threat display, and then thoroughly washed. For the purpose of manoeuvring it in the water the preserved fish was fixed to one end of a strip of organic glass which was 1 m. long and 10 mms. wide. — The two fishes chosen for the experiment had their stations upon the same imaginary line which was perpendicular to the direction of the current. The distance between the stations was 34 cms. With the aid of the photographic map of the bottom 5 uniformly spread experimental places, viz. A, B, C, D, and E, were identified upon the straight line connecting the

Fig. 3. Aggressiveness of two salmon fry with territories bordering unto each other. In the upper diagram ▷ and ◁ mean single attacks against the dummy from the left and right fry, respectively. In the lower diagram the total numbers of attacks are shown for each of the five experimental places.

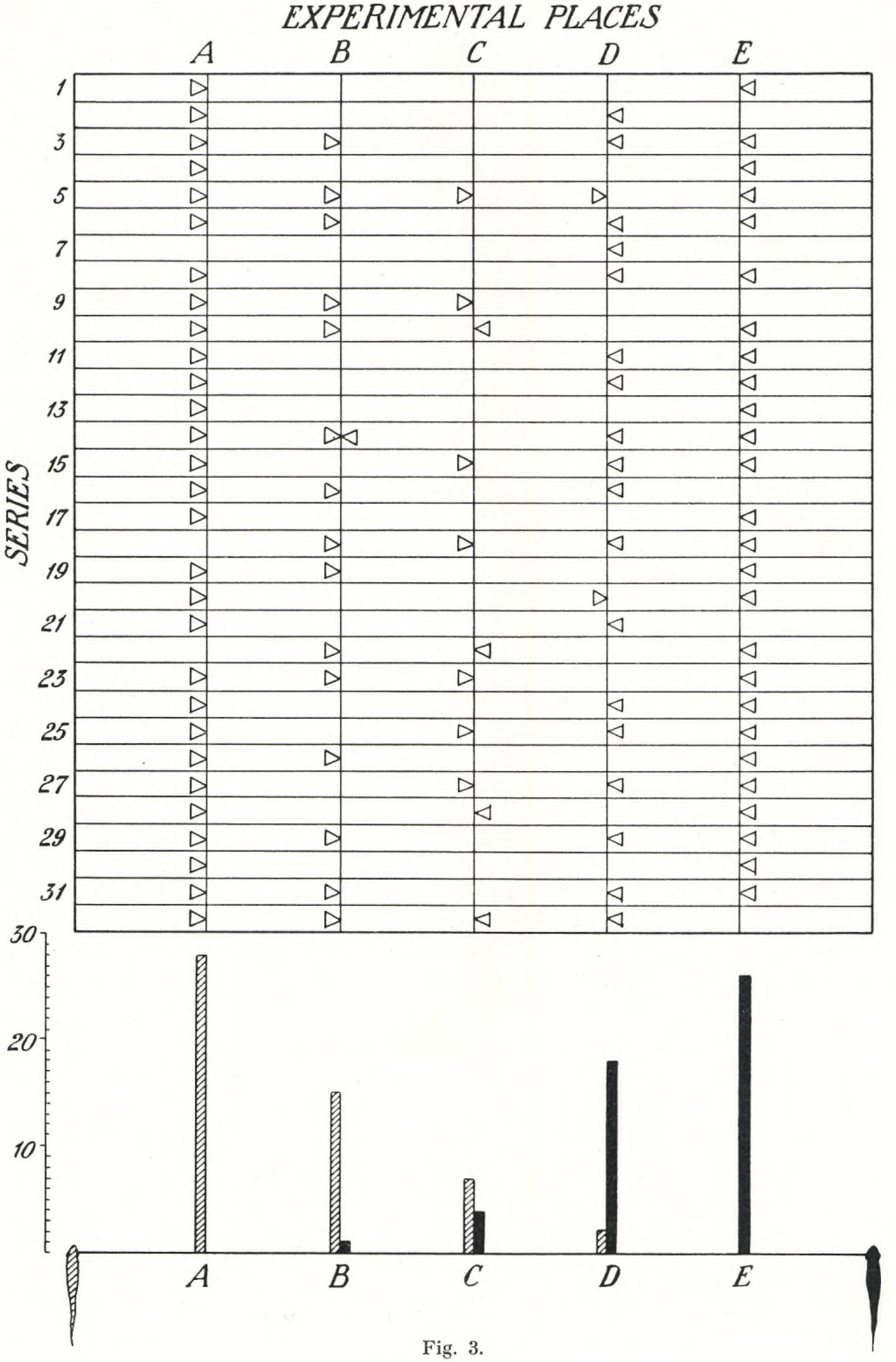
EXPERIMENTAL PLACES
A
B
C
D
E
SERIES
1
3
5
7
9
11
13
15
17
19
21
23
25
27
29
31
30
20
10

Fig. 3.

two stations. Every other minute the dummy was shown in one of the experimental places. In every instance it was lowered vertically towards the bottom while being kept parallel with the experimental fish. It was held close to the bottom for the space of 5 seconds, and then withdrawn from the water. The presentation at the different places followed the sequence CBDAE, CDBEA, AEBDC, and EADBC, two times and this scheme was repeated each day until the dummy had been shown altogether 160 times. This led to the registration of 101 attacks or intention movements for attack. The aggressiveness of the two experimental fishes was the same (52 and 49 attacks, respectively, $\chi^2=0.89$). All the time the salmon fry exhibited very little interest in the slow movements above the surface of the water. The diagram (Fig. 3) shows that aggressiveness to have been greatest upon the station, and to have decreased continuously in centrifugal direction. The areas of interest of the two salmon fry overlap in a wide transitional zone. To this picture of the nature of the boundaries of the juvenile salmon territory — and nothing suggests that brown trout should behave in a different way — we can apply DIESSELHORST's (1949) characterization based upon the territory of the yellowhammer (*Emberiza citrinella*): "Das Revier ist für den Vogel nicht, wie für den Menschen sein Garten, ein in allen Teilen gleichwertiger Besitz, von der Aussenwelt durch einen Zaun abgeschlossen, sondern es besteht eine Art Konzentrationsgefälle in der Intensität der Verteidigung, . . . von bestimmten Schwerpunkten nach aussen hin, wo sie allmählich verebbt." If, however, the topography of the bottom was more broken with regard to the size of the fishes, parts of the boundaries of the territories could appear with extraordinary distinctness. This was the case, e.g., where an intruder under cover of a larger stone could approach the station quite closely, but was regularly attacked as soon as it had passed the stone.

Fig. 2 shows the territories to have a tendency towards eccentricity, probably a result of the fact that the fish more easily notices an intruder in upstream direction, i.e. in front of itself.

The territories of juvenile salmon and trout must be designated as pronounced bottom territories. Numerous observations have shown that in the open water strange fishes could pass the station without being attacked at much closer quarters than what was possible along the bottom. Similar conditions seem to prevail in the territories of cichlid fishes (BAERENDS and BAERENDS 1950). With the parr of salmon and trout the small vertical extent of the territories is remarkable, since the feeding excursions are directed mainly towards the open water (cf. p. 70 and Fig. 5).

The diffuse boundaries of the territory can be attributed to the existence of a fixed station and to the relative immobility of the fish within the territory connected with it. Distinctly limited territories have admittedly been described for fishes, but in these cases the territorial behaviour regularily seems to include a more or less pronounced patrolling activity. Such territories occur with the cichlid fishes (BAERENDS and BAERENDS 1950), but are found also, and perhaps more developed, in the bream (*Abramis brama*), where "the strikingly restless movement of the males patrolling their territories" (FABRICIUS 1951) takes place "continuously for several hours" (SVÄRDSON 1949 b). Also the char (*Salmo alpinus*) patrols his spawning territory (FABRICIUS and GUSTAFSON 1954), but less intensively than the bream. In the grayling (*Thymallus thymallus*), which spawns in running water, the male is rather strictly bound to a station, and the patrolling activity is therefore still less pronounced. Quantitative informations supplied by FABRICIUS and GUSTAFSON (1955) show, however, that also the grayling is much more moveable within its territory than the parr of salmon and trout which latter, apart from the feeding expeditions, can lie for many hours upon the stations. It might be justifiable to speak about two extreme types of territories in the fishes, viz. the distinct patrolled territory, and the diffuse station territory.

With the parr of salmon and trout the territory must be considered as being of a rather simple organization, mainly on account of the pronounced centralization of all activity to the station. Highly organized territories which show good correspondence to those of birds and mammals have so far been described in fishes only for *Serranus scriba* of the Adriatic (KIRCHSHOFER 1954).

On account of the centrifugally decreasing gradient of aggressiveness which characterizes the territory it appears devoid of meaning to speak of a definite size in the case of a solitary territory upon smooth uniform bottom. In the aquarium (as well as within suitable biotopes in nature) closed territorial mosaics were, however, often formed in which each individual was in aggressive contact with its neighbours. Only in such mosaics it is possible to carry out at least a simple estimation of the average size of the territories by dividing a representative part of the bottom surface by the number of fishes which there defend territories.

This average size of the territory depends of course in a high degree upon the size of the defending fish. Salmon fry which had emerged from the gravel a month ago defended territories of 2—3 sq. dms., while large parr and smolts frequently had territories which extended across the entire width of the aquarium, and could cover more than 1 sq.m. A trout of 23 cms. held sway over more than half of the bottom surface (about 4 sq.ms.), the aquarium containing at the same time also 11 parr of salmon and trout of about 15 cms.' length.

It is a well known fact that also in fishes the size of the territory is connected with the degree of visual isolation within the biotope. It has been shown that the topography of the bottom and the vegetation can have a screening effect within the population, and permit an increased density of colonization (FABRICIUS 1951, KIRCHSHOFER 1954, FABRICIUS and GUSTAFSON 1955, FORSELIUS 1957). When by placing some larger stones upon the bottom

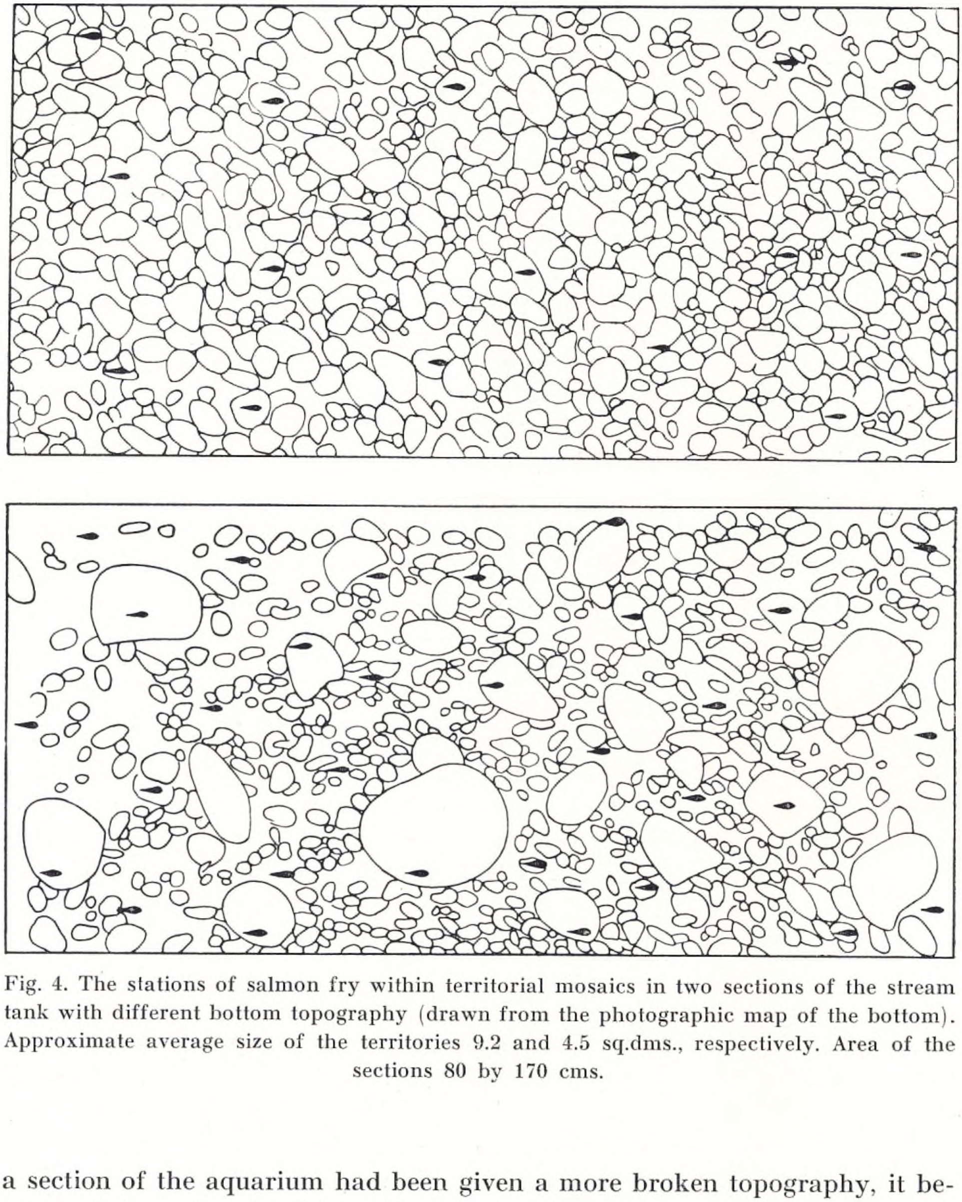

Fig. 4. The stations of salmon fry within territorial mosaics in two sections of the stream tank with different bottom topography (drawn from the photographic map of the bottom). Approximate average size of the territories 9.2 and 4.5 sq.dms., respectively. Area of the sections 80 by 170 cms.

a section of the aquarium had been given a more broken topography, it became obvious that in this section the territories were smaller than in the remainder of the aquarium (Fig. 4).

During experiments on intraspecific competition carried out in July 1957 about 400 salmon fry were kept in the aquarium. At this high population density (1 ind./1.7 sq.dm.) only about $^2/_3$ (roughly 250 individuals) of the fry occupied normal territories (average size 2.7 sq.dms.). Between July 12 and July 26 the number of fry occupying territories was counted every day between 10.00 and 11.00 a.m. The velocity of the water current was kept steadily

Table 1. The number of territorial salmon fry at high density of population; before, during, and after a period of increased velocity of current. Total number of fry about 400.

Current	18 cms./sec.					29 cms./sec.					17 cms./sec.				
Day in July 1954	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Number	244	259	264	236	253	280	298	289	261	279	243	262	234	247	255
Average	251.2 ± 5.012					281.4 ± 6.153					248.2 ± 4.731				

The average at 29 cms./sec. is significantly separated from the averages at 18 and 17 cms./sec. ($t=3.79$; $f=8$; $p < 0.01$, and $t=4.24$; $f=8$; $p < 0.01$, respectively).

at 18 cms./sec. until July 16 when in the course of the afternoon it was gradually raised to 29 cms./sec. On July 21 the velocity of the current was in the same way lowered to 17 cms./sec. The results, which are tabulated in Table 1, show that during times of increased velocity the number of individuals occupying territories was greater, i.e. that the average size of the territories became smaller. This can be interpreted as an effect of the depression of the stations by the increased velocity of the current. This depression increased the visual isolation, and enabled fry which previously were without territories to occupy such within the population. When the population density was great, an increased turbidity in the aquarium brought with it a noticeable increase in the number of fishes occupying territories, i.e. also in this case a decrease in the size of the territories. The difficulties of observation in the turbid water did, however, not permit quantitative investigations. (Cf. also p. 59 about the choice of stations at high turbidity.)

D. *Fixation to the territory*

In the aquarium it was easy to establish that salmon parr of different sizes occupied their territories for a considerable time. Although no attempts have been made to determine the maximum duration of the territories under aquarium conditions, I shall nevertheless report on some observations.

In July 1956 the stream tank contained about 100 fry of salmon which had been hatched in the aquarium. Individual characteristics in the pigmentation permitted me to recognize 18 of them which had their territories close to the glass panes. During 23 days the positions of the stations of these 18 fry were registered almost every day. During this time 4 of the fry disappeared beyond the distance required for identification, implying in the case of these small fishes that their distance from the glass pane was more than about 40 cms. Of the remaining fry 3 moved their territories for a distance of at most 230 cms., either up-stream or down-stream, while 11 fry retained their stations right through the entire period of observation.

When, in the summer of 1955, the aquarium for a certain time contained in addition to a varying number of yearling salmon also 6 salmon parr of two years, two of the older parr were observed to keep to their stations for at least 59 days.

In the end of July 1956 a number of salmon fry were transferred for the purpose of a particular investigation from the stream tank to an ordinary aquarium with gravel bottom and without current, its size being 40 by 50 cms. In this aquarium the fry did not occupy territories, but aggressiveness was nevertheless observed. Two of the fry belonged to the group of fishes which were individually recognizable. After a stay of four days in the small aquarium they were re-transferred into the stream tank. On the following day one of the fry was seen there. It had now retaken possession, not of its latest territory, which it had occupied during its 7 last days in the stream tank, but of that which it had earlier defended during 19 days.

The fixation of the fry of salmon to the stations becomes obvious, when attempts are made to drive the fish from its territory, e.g. with a stick. When in such attempts the stick came close to the station, the fish fled for only some decimetres (sometimes after having attacked the stick!). At greater distance from the station, i.e. when, generally speaking, outside its territory, the fish no longer fled from its station, but attempted to pass by the stick, and to regain its territory. At a distance of about one metre from the station this tendency to regain the territory was so strong that it demanded the greatest attention to prevent the fish from succeeding. In this way, and on different occasions, 13 individually recognizable fry were chased 3—6 ms. downstream from their stations. One of the fishes occupied a new territory in the neighbourhood of the spot to which the flight had taken it. Two of the fishes could not be rediscovered in the aquarium, and must be supposed to have occupied new stations at distances greater than about 40 cms. from the glass pane. The remaining 10 fry reoccupied their original territories. The time for these movements varied widely, from less than one minute to two days. In some cases it could be observed directly, how the fry immediately worked its way up-stream, close to the bottom and under incessant fights with the occupants of the territories through which it had to pass. After the fry had reached its own territory or its vicinity it moved directly to the station in a way which indicated its intimate acquaintance with the topography of the bottom.

At moderate population density and normal velocity of the current all juvenile salmon and trout in the aquarium occupied territories. Nothing indicates that under such conditions individuals without territory ever occur. Informations about down-stream drift, schooling, obvious mobility, etc. of fry and parr of salmon or of other territorial salmonids are, however, numerous (HUNTSMAN 1945, HOAR 1951, STUART 1953, LINDROTH 1956 etc.). When territories are finally abandoned, the reason can be increasing competition pressure within the population (p. 88), or that the individual simply has "outgrown" its environment, or changes of the water current. Especially the velocity of the current influences the life of the juvenile salmon and trout in many ways: it directly acts upon aggressiveness and territoriality (p. 82), forces the fish by purely mechanical action to leave exposed stations and biotopes, and acts on account of the special adjustment of juvenile salmon and trout to drifting prey also upon the supply of food (p. 69).

IV. The Activity of the Fish within the Territory

A. *Feeding activity*

The territories of juvenile salmon and trout are feeding territories. Their small size and long duration lead, however, to the inevitable conclusion that the fish can not possibly subsist on the bottom fauna of the territory. As far as the trout is concerned MÜLLER (1954) and NILSSON (1957) have also clearly shown that in running water it feeds essentially on the "organic drift" (MÜLLER 1954) carried along with the current. This important fact was apparently realized already by NORBÄCK (1884). He wrote: "During the early period of its life, after it has consumed the yolk bag the young salmon fry stays perfectly quiet in its hiding place among the stones of the bottom, and is constantly supplied by current and eddies with the small crustaceans which during this period serve for its food . . ."[1] In the stream tank no differences have on the whole been observed between the feeding behaviour and the choice of food of salmon parr and trout parr, respectively. Both species were almost exclusively intent on prey animals from the drift, irrespective of their origin (benthos, plankton, air fauna).

The feeding behaviour of the trout, well known to the amateur fisherman, has been described by FABRICIUS (1953 b) and MÜLLER (1954). HUNTSMAN (1954) noticed the feeding excursions of salmon smolts in the estuary of the Margaree River.

In the course of its typical feeding excursions the juvenile salmon or trout rushes with lightening speed from its station at the bottom obliquely upwards into the open water, where the observed prey is caught hold of with a sudden turn. The fish then regains its station. Here somewhat larger prey is further dealt with: the prey is shaken, spat out, again taken into the mouth, etc., until it is either finally swallowed or definitely rejected.

Feeding excursions aimed at prey animals upon the bottom are rare, and then carried out as a rule quite close to the station. The prey can consist of small larvae of insects, but the behaviour follows the same pattern, when

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[1] Translated from the Swedish.

larger parr of salmon or trout are hunting for fry. Often, however, the prey is non-existent or is represented by a small stone, the size of a pea, or of a tuft of algae or the like, giving displacement character to the activity. The behaviour of the fish during excursions for food near the bottom markedly differs from that observed in the course of all other feeding, and is of a certain ethological interest (p. 75): the fish approaches the prey with its dorsal fin lowered and with increasingly arched dorsal profile, brakes up the motion by means of the paired fins, fixes the prey steadily with its eyes, and catches it with a violent movement.

In summer-time the chase of flying insects by salmon and trout parr can become of considerable extent. This chase could be followed in the aquarium, when during warm evenings the insects swarmed in through the open skylights. The excursions against prey upon or above the surface of the water are often preceded by an introductory moment, the fish placing itself in the position of departure for the rectilinear upward rush through the surface of the water. In shallow water the rush is started directly from the station upon the bottom. With regard to the visual achievements during this chase the juvenile salmonids are hardly inferior to the frequently mentioned archer fish (*Toxotes jaculator*). Salmon smolts successfully hunt swiftly flying insects close above the surface of the water (*Mystacides!*), and catch with precision slower flyers at heights up to 40 cms. As for *Toxotes* we must postulate also in this case great visual acuity and ability of estimating direction and distance, inclusive of correction of the refractive phenomena in the surface of the water.

Under normal conditions the feeding range in horizontal direction corresponds roughly to the size of the territory, whereas in vertical direction the excursions for food are extended beyond the territory (p. 64 and Fig. 5). During intensive hunting of flying insects, however, the general behaviour of the fish in the aquarium underwent marked changes. At moderate velocity of the current (about 15 cms./sec.) larger parr of salmon and trout left the bottom, and spent the intervals between the jumps in open water, without, however, leaving the normal feeding range. Observations made in July 1956 in the brook near the laboratory indicate, however, that during intensive hunting of flying insects trout parr can stray far from their territories. Two trout parr (of about 10 and 15 cms.' length) had their stations in the brook, 8 and 12 ms. above a pool. As a rule the fishes were easily found upon their stations. Only twice during the course of altogether 14 observations made in the evening (7.00—8.00 p.m.) this did not succeed. These two evenings were remarkably warm, and in the pool down-stream small trout jumped eagerly after flying insects. Between the jumps the fish were seen roaming near the surface of the quiet water. (Some of the fish were possibly salmon parr.) When the brook was visited on the following morning (7.00 a.m.) the two

Fig. 5. Digrammatic profile through territory and normal feeding range in juvenile salmon and trout. The shadowing is intended to show the centrifugally decreasing aggressiveness within the territory. Broken line shows extension of the feeding range.

trout parr were seen again to occupy their stations, and only the usual brief feeding excursions were observed. I supposed that in the hunting of swarming insects the trout parr had been carried down-stream by the current, until they came to rest in the quiet water of the pool, where the hunt was continued. Such a "feeding migration" constitutes a marked deviation from the otherwise strict fixation to the territory.

Several authors have established the occurrence of diel rhythm in the feeding activities of salmonid fishes. Feeding experiments (HOAR 1942, OLIPHAN 1957) show the activity to be at a maximum in the mornings and evenings, and lower during day-time, in order to cease altogether in the night. During the darker part of the year the juvenile salmon in the aquarium complied well with this scheme. Feeding took place right through the day, but often less intensely around noon. Both length and frequency of the feeding excursions increased towards sundown. The maximum was reached some time after sunset. With increasing darkness the feeding intensity diminished at a fast rate, the excursions became shorter and shorter, and were separated by longer intervals. When the illumination was so feeble (much less than 0.02 lux at the surface of the water) that the fish could no longer be traced in the aquarium, the chase ceased entirely. Inspection with an electric torch showed that after the termination of the chase the fry had left their stations, and hid between the stones of the bottom (p. 61). With the intensification of the light towards the morning the excursions were resumed, and reached a new maximum. During the light nights of the summer, when the illumination at this latitude (about 63°N.) frequently surpassed 25 lux at midnight,

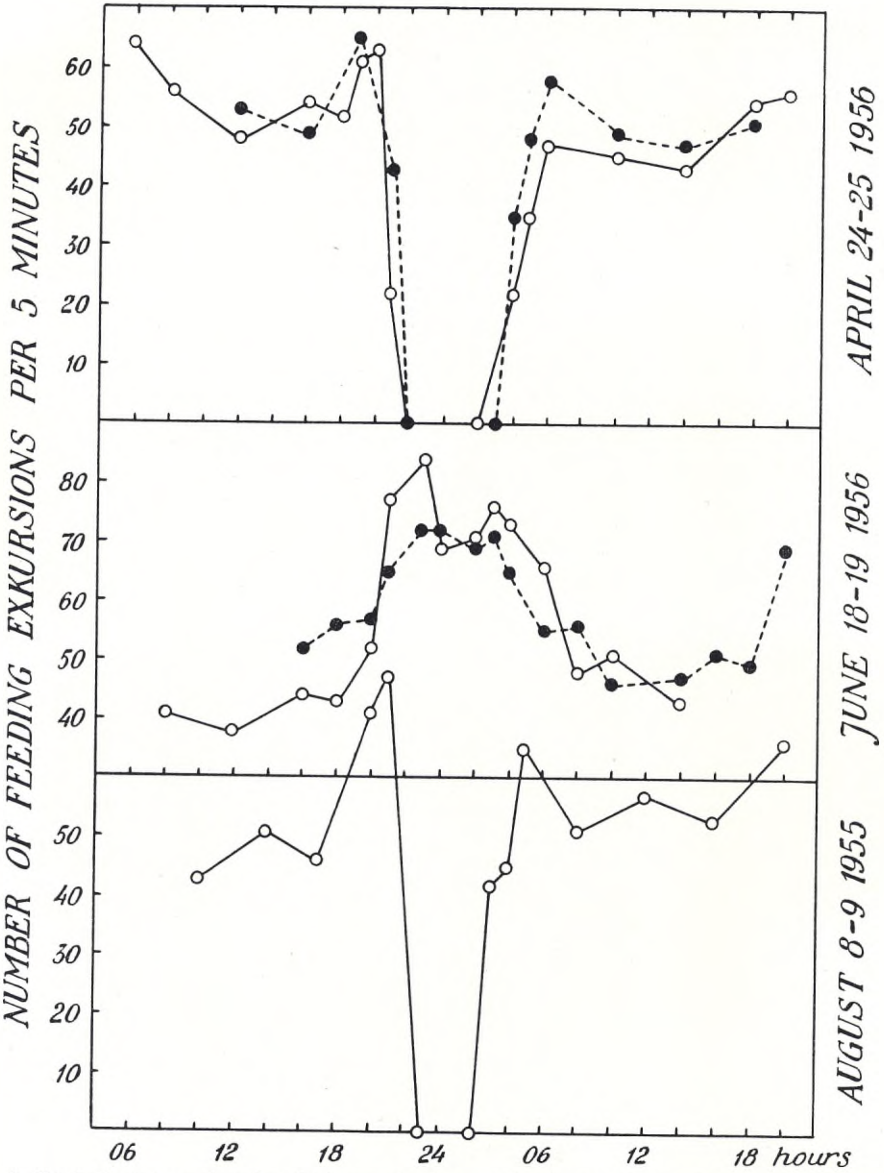

Fig. 6. Typical curves showing 24-hour rhythm of feeding activity of salmon fry in the stream tank at three different times of the year.

the picture differed from that drawn up in the foregoing. The morning and evening maxima were retained, but the excursions were continued with high intensity right through the night (Fig. 6). As had been observed also by HOAR (1942) the rhythm of the feeding activity lagged behind the rhythmical sequence of the illumination. It can be mentioned that under experimental conditions the diel rhythm of the smolt migration is out of phase in the same direction (KALLEBERG, unpubl.). In a preliminary note about underyearling coho salmon feeding on *Daphnia* under experimental conditions BRETT (1957) mentions that "the level which just produced a significant reduction from the normal rate of feeding was approximately 0.0001 ft.c." (corresponding to 10^{-3} lux). There is no reason to suppose that the scotopic vision of juvenile Atlantic salmon should be much inferior to that of the Pacific species and, consequently, that in the stream tank the fishes made use of anything else than visual feeding.

B. *Agonistic activity*

The territory is defended by its owner which by aggressive actions attempts to chase away intruders. The term "agonistic behaviour" was introduced by SCOTT and FREDERICSSON (1951) as a collective designation of attack and flight reactions.

1. *Agonistic displays*

In the course of the aggressive contacts real fighting is replaced to a large extent by sham fighting by means of threat displays. These are complex, at least mainly visual signals built up of a varying number of elementary actions. The threat value increases with an increase in the number of the involved elements and/or with an accentuation of the different elements. Existing descriptions of the agonistic behaviour of salmon and trout are based, for the salmon exclusively and for the trout mainly, upon studies of the territorial fights of grown-up fish in connection with spawning (JONES and KING 1949, 1950, 1952, STUART 1953, JONES and BALL 1954, FABRICIUS and GUSTAFSON 1954, FABRICIUS 1955). These descriptions show the trout to exhibit a considerably more complicated pattern of actions than the salmon. In juvenile salmon and trout conditions seem to be different. I have not observed any certain qualitative differences in the threat displays. While thus salmon as parr (fork-length about 7 cms. or more) and as smolt exhibits complicated threat signals which have no correspondence to what I have observed in the stream tank in the course of the spawning of adult salmon, conditions for trout are in some sense the opposite: certain elementary threat actions, especially the erection of the gill covers and the branchiostegal membranes, are of much greater intensity in older individuals (STUART 1953, FABRICIUS 1955) than in parr.

The frontal threat display (Fig. 7 a, Fig. 8) is usually made, while the fish is swimming forward. With closer approach towards the opponent the dorsal profile of the fish becomes increasingly convex (like a cat

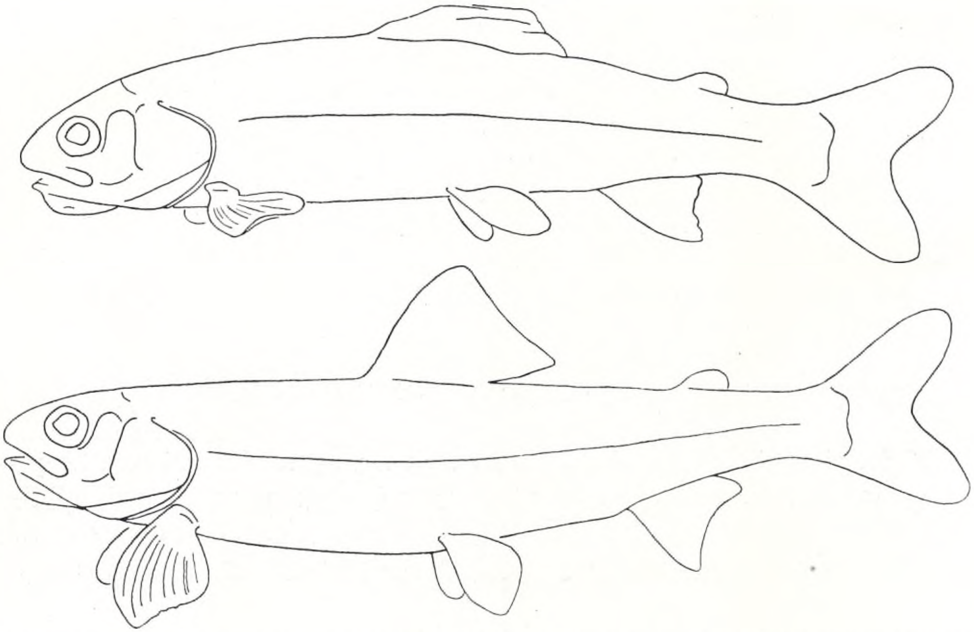

Fig. 7. Sketches of frontal (a) and lateral (b) threat displays in juvenile salmon and trout.

arching its back). The dorsal fin is kept lowered, while all the other fins are extended. The mouth is open. Operculum and branchiostegal membrane are at least somewhat extended (cf. above), and the bottom of the mouth is dilated downwards in the shape of a light-coloured shallow pouch.

The frontal threat has a highly aggressive character. It is of short duration, not exceeding a few seconds every time. With trout parr it is often concluded by a bite, i.e. the threat leads to real fighting. In salmon parr the frontal threat is of lower intensity. In them the erection of the fins is seldom seen as complete as in trout parr, and normally the mouth is not opened before the concluding phase, when the salmon parr executes the threat bite in the water near its antagonist. The gular pouch, which is very prominent in trout parr, is much smaller in the parr of salmon.

In both species the frontal threat is often seen in qualitatively incomplete condition. Already the approach without threat display has a distinct threat value. The arching of the back, however, and the characteristic lowering of the dorsal fin are rarely absent.

What has been called "nipping" by HOAR (1951) can be interpreted as a simplified frontal threat, a darting approach which is usually followed by threat bite.

According to an opinion which has found wide acceptance among ethologists the threat displays result from a conflict between tendencies towards

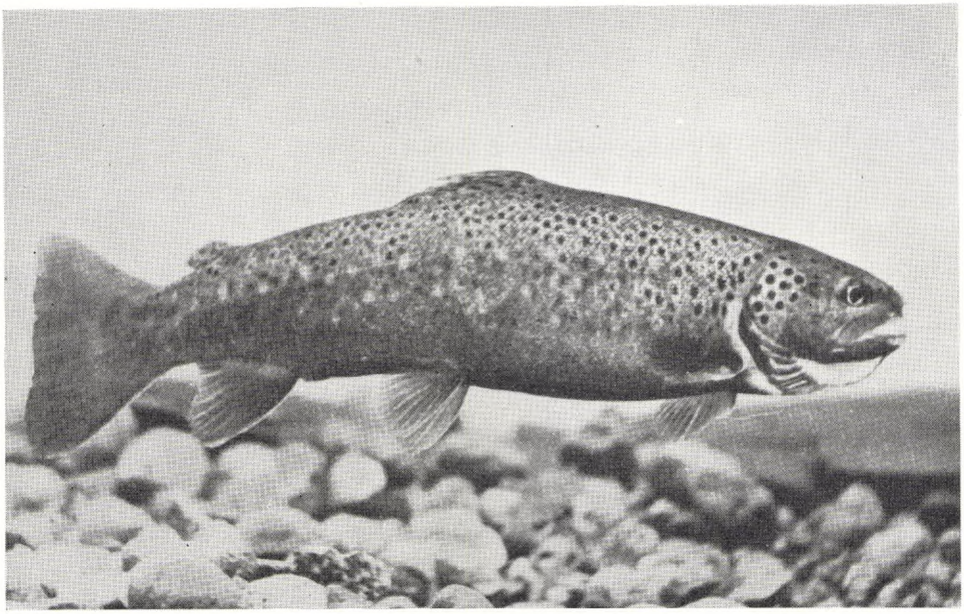

Fig. 8. Frontal threat display in grown-up brown trout. Note the arched back, the lowered dorsal fin while all other fins are erected, the erected gill cover complex, the gular pouch, and how the threatening fish fixes its adversary with its eyes. — Photogr.: K.-J. Gustafson.

attack and flight. Thus Fabricius (1953 a) writes about the erection of the fins: "Most probably the erection of the fins in the display of the char has been derived from braking movements, originally released by the increased strength of the escape drive in the attacking or courting fish when it approaches its opponent or partner." The extraordinarily great similarities existing in salmon and trout parr between the frontal threat display on the one hand and the posture of the fish on the other, when swimming towards a prey animal upon the bottom (p. 70), suggest, however, the assumption that in these fishes the frontal threat is to a large extent composed of elements of the feeding behaviour. Before the prey is finally caught a conflict between "approach" and "escape" is often very obvious in the behaviour of the fish. A salmon fry could approach e.g. a Plecoptera nymph, 10—12 mms. in length, several times, but retreat again every time. Occasionally the fry returned to its station. After several approaches toward a large prey a salmon fry may even show typical displacement activities (nipping on stones, tufts of algae, etc.). In the moment of the feeding excursion, when the fish, after the onrush, brakes, steadily fixes the prey with its eyes, and opens the mouth in order to catch it, the frontal threat display is as a matter of fact fully developed. It has to be remembered, however, that the lowering of the mouth bottom and the movements of the gill covers and the branchiostegal membranes all result from the same muscular contractions that also open the mouth. These actions at frontal threat differ in no way from what is observed, when the fish yawns, or when it opens the mouth in order to catch its prey. The mechanism of the jaw and branchial apparatus in connection with threat displays has been studied in *Tilapia* by BAERENDS and BAERENDS (1950). By experimenting with preparations of salmon and trout one can easily convince oneself that in these fishes the conditions are in principle the same. Contraction of the m. coracohyoideus draws the hyoid arch backward and downward, and by the transmission of this movement to the jaws the mouth is opened. And when the median portion (copula) of the hyoid arch moves downwards, it depresses the bottom of the mouth into the formation of the characteristic gular pouch, while the simultaneous longitudinal backward movement forces the gill cover complex in lateral direction. In parr of salmon as well as of trout frontal threat displays with distinct gular pouch occur, yet without opening of the mouth. In a superficial way this can be interpreted as omission of an action, viz. of the opening of the mouth, but our knowledge of the mechanics of the jaw and branchial apparatus makes us realize that in fact a new action has been added, viz. the closing of the mouth, effected by the contraction of the m. adductor mandibulae. From the ethological point of view this is an interesting phenomenon: The opening of the mouth as ingress to the bite is most probably a very primitive threat, into which, however, the derived passive actions (lowering of the mouth bottom, erection of the gill covers etc.) have entered as such essential features of the visual signal that the threat value, though with reduced intensity, remains even when the mouth is closed, and the intention of biting is no longer apparent. When the mouth is kept closed in connection with a threat display, we can reasonably consider this attitude as the result of a distinct action, perhaps as the consequence of flight tendencies.

The lateral threat display (Fig. 7 b) exhibits great similarities with the corresponding position in char and grayling (FABRICIUS 1953 a, FABRICIUS and GUSTAFSON 1954, 1955). The back of the fish is stretched beyond what is normal, the lateral line, which in normal posture is straight, appearing upwardly concave. All fins are extended as much as possible. The bottom of the mouth is dilated and lowered so as to form a gular pouch, and the gill cover complex is at least partly raised. The mouth is, however, always almost completely closed. When the lateral threat is displayed on the spot, a movement, resulting in a distinct increase of the threat value, is sometimes added. In this movement the rigid body of the fish is seen to oscillate violently around a vertical axis. The amplitude of this movement is about 15 degrees, and the frequency about 0.5 oscillations per second.

The lateral threat display has a clearly defensive character. It is also of longer duration than the frontal threat. In salmon parr of about 14 cms. length the average duration, calculated from 26 measured displays, was

6.4 seconds. In certain cases, however, the lateral threat can be displayed during 2—3 minutes (mutual display, see below). Like the frontal also the lateral threat display is found to be stronger in trout parr than in salmon parr. The reason lies in an accentuation of the different threat elements. Only the erection of the fins and the closed position of the mouth are about equally apparent in both species. The closed condition of the mouth has, in relation to the other movements of the jaw and branchial apparatus, to be considered as a distinct action, as already pointed out in the foregoing.

The lateral threat display has the character of a general tonic spasm which makes one think of the "decerebrate rigidity" of the higher vertebrates. A similar spasmic condition can be observed, e.g. in a trout for a few seconds after it has received a hard blow upon the head: over-extension of the vertebral column, general erection of the fins, extension of the gill cover complex. Similar passing phenomena are observed as results of electrical shocks (electrofishing!). The spasticity of the lateral threat display is strong enough to make normal swimming movements impossible. The previously described rigid oscillation is perhaps identical with the undulatory movements on the spot which are often seen in salmon and trout parr under normal tonic conditions.

For the trout JONES and BALL (1954) have described what they consider as a possible "dominance posture" in which the fish "postured at about 45° to the horizontal with head high and tail touching the gravel". It is obviously unreasonable to expect that in this position a fish should be able in stronger current to maintain its position in relation to the bottom. On the basis of the data supplied by JONES and BALL (op. cit.) the velocity of the current at the occasions, when they observed the dominance posture, can be calculated to about 5 cms./sec. In the stream tank of the Salmon Research Laboratory the velocity of the current was kept normally at 18—25 cms./sec., and under these conditions no dominance posture was ever observed. It could, however, be brought about, at least in larger trout parr, by a lowering of the current velocity to almost zero. When this was the case, the fish ascended into the open water, and collected in the up-stream section of the aquarium (p. 84). Also the trout which had its territory in this part of the aquarium rose into the open water, and attacked the other fishes, when they assembled there. Between the attacks the defending trout swam about in a peculiar, halfway erect position which agreed well with the description given by JONES and BALL (op. cit.). Erection of the fins or similar actions did not occur. If the depth of the water was sufficiently great, this behaviour was observed only, when the fish was in the open water. The assertion of JONES and BALL to the effect that the tail fin of the fish touched the bottom can probably be connected with the small depth (less than the length of the fish) in their aquarium.

When on flight parr of salmon and trout drop all their fins in a very characteristic way. This submissive display is well known for most of the territorial fishes which have been studied.

2. *Fights and sham fights*

Real fights, with physical contact between the opponents, occur in trout of all stages of development, and comprise pushes and rapid bites. Sometimes also a holding-on to the fins of the opponent during considerable time is observed.

In salmon real fights occur both among fry and, though less frequently than among trout (*fide* JONES and BALL 1954), also among adult individuals in connection with territorial conflicts upon the spawning places (p. 82). Among larger salmon parr the real fights are almost completely replaced by sham fights.

Also in the cases in which the owner of the territory does not immediately react with a threat display, the eye movements of the fish easily allow the conclusion that the intruder has been discovered. On condition that the intruder remains passiv, this initial stage can last up to some minutes during which the defending fish gazes frequently at the intruder. Simultaneously intention movements towards approach are observed: the fish turns its head towards the intruder or drops the dorsal fin, and approaches by one centimetre in order immediately to regain its station. On one occasion a salmon parr was observed in the aquarium which became increasingly irritated on catching, during some minutes, repeated glimpses of its neighbour through a gap between two stones. The intention movements towards approach became more and more pronounced. Four times in rapid succession the salmon parr made feeding excursions towards non-existent prey upon stones near the station, each of them followed by prey-shaking. Half a minute later a swift feeding excursion took place during the course of which the fish tore off a small tuft of *Batrachospermum* which had been growing during at least two weeks upon a stone at a distance of 5 cms. from its nose. The fish then returned to the station, shook the alga, and finally spat it out. These actions as well as the frequently occurring yawnings and chafings against the bottom, observed in similar situations, must be considered as displacement activities.

In the face of a suddenly appearing intruder the defending fish reacts either with a lateral display or by an immediate approach, often without frontal threat display. The lateral threat is displayed mainly against intruders which have been observed down-stream or at the sides. If thereupon the intruder does not retreat, the defender intensifies the threat by the execution of the stiff oscillating movement. Against down-stream intruders the fish lets itself be carried with the current, tail first, as has been described by JONES

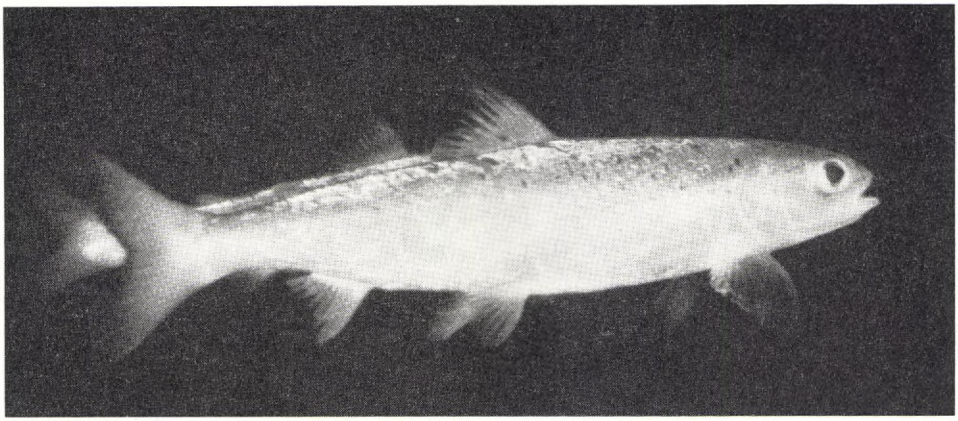

Fig. 9. Mutual lateral threat display (parallel-swimming) of moderate intensity in salmon smolts. The photograph was taken 1 1/2 hour after the netting of the fishes from a school of actively migrating smolts (Fig. 12).

and KING (1950, 1952), JONES and BALL (1954), and FABRICIUS and GUSTAFSON (1955).

In the aquarium it has repeatedly been observed that salmon and trout parr resisted reiterated pushes and bites on the part of the antagonist, reacting each time with a marked intensification of the threat display or by the execution of the stiff oscillation.

When a lateral threat induces the same action on the part of the opponent, the situation arises that the fishes occupy parallel positions, both facing the current. This mutual, very intense threat is usually interrupted after a few seconds, one of the fishes changing to frontal threatening or direct attack. It can, however, happen that the opponents, while still retaining the strict parallelism, start to move against the current. In this case the tail fin carries out vibrating beats of high frequency, but with extremely small amplitude. The appearance is created as if the two fishes, under mutual threat display, slid along two parallel threads through the water. In the aquarium the distance between the fishes could amount to thrice the length of the fishes, but frequently the individuals almost touched one another (Fig. 9).

During mutual threat display it is often noticed that one or both fishes rotate about their longitudinal axis up to 45 degrees. In 18 observed cases the direction of the rotation did not, however, show any regularity. The deviation from the normal posture might possibly only be a consequence of the circumstance that during very intense lateral threatening the fish can not fully control its position in the water.

During the parallel swimming no boundaries between territories are respected. When strange territories are traversed, one or two fishes can join in. On one occasion three salmon smolts were seen swimming parallel and close to each other along the whole of the aquarium showing all the time an intense lateral display. Often, however, the fishes move in open water, high above the bottom, and thus attract but scant attention on the part of the other fishes (p. 64). Parallel swimming accompanied by lateral display is well known in salmonid fishes (FABRICIUS and GUSTAFSON 1955, and the references given in this paper), and has been described in almost identical development for *Rasbora heteromorpha* (WICKLER 1955).

The contest in the aquarium carried the fishes far outside their own territories. This was the case first of all in connection with the parallel swimming, and when one fish pursued another. In parr of salmon as well as of trout it also happens at long intervals that these defending fishes spontaneously leave their stations for excursions which can extend through numerous strange territories. During such an excursion the fish can pause, and for half an hour defend a temporary station far outside its own territory. These distant excursions do not seem to have any clear function in the defense of the territory, and can not be compared with the patrolling of the territory as it occurs in typical form e.g. in cichlid fishes. Somewhat similar excursions have been observed in char and grayling, and have been interpreted by FABRICIUS and GUSTAFSON (1955) as an "appetite behaviour for fighting". Since the fish normally, sooner or later, returns to its station, it must be supposed to possess considerable local knowledge extending over an area of the bottom which greatly surpasses the extension of its territory.

V. The Development of Aggressiveness and Territoriality in the Individual

For the purpose of studying at close quarters the first appearance in fry of feeding behaviour, aggressiveness, and territoriality a simple small stream tank with a bottom surface of 19 by 80 cms. was constructed. The material covering the bottom was sand and gravel (diam. 1—6 cms.) with a thickness of about 15 cms. The depth of the water above the surface of the gravel varied between 18 and 23 cms. This variation was the result of the clogging between the cleanings of the fairly finemeshed grating of the aquarium. In connection with it the velocity of the current in midstream, determined as the average velocity in the uppermost 10 cms. of the water, varied between 20 and 17 cms./sec. The aquarium was stocked with 20 hatching eggs of salmon or trout. After the emergence from the gravel of the first fry several observations were made every day during the two following weeks.

Observations of behaviour elements in fry are made difficult mainly by two circumstances, viz. the small dimensions and the short lapse of time within which things happen. These difficulties of observation bring about an obvious risk that the behaviour of the fry will be perceived too schematically. The problem can be mastered only by means of ultra-rapid motion pictures of the movements. As the author had no access to the necessary equipment he had to desist from comparing in detail the threat displays of the fry with those of larger fish.

During the first days after their emergence from the gravel the fry in the aquarium were seen collected in clusters between the stones, and not exhibiting much activity. Occasional feeding excursions with a reach of a couple of centimetres could, however, occur already during the first day. 3—4 days later feeding was common among the fry. This feeding at first took place without a perceptible choice of the prey, all kinds of particles being seized, provided only they were in motion, from small air bubbles and occluded debris (often including diatoms) to full-grown larvae of *Simulium.* The fact that also air bubbles are caught is of special interest (p. 91). Feeding excursions directed against objects upon the bottom seemed to be commoner in these young fry that in larger fish, and were, as in the latter, carried out with an exaggeratedly convex profile of the back.

During the first two weeks the feeding behaviour exhibited an increasing specialisation by being to a larger extent directed towards the open water, while at the same time the fry was surer to choose edible objects.

In a number of cases salmon fry was observed to show aggressive behaviour already during the first day after the emergence from the gravel. Only fry which had started to feed exhibited aggressive behaviour. The aggressiveness led to the dispersal of the clusters. Afterwards the momentary places were soon established as more or less permanent stations from which the first territories were defended.

The aggressive behaviour of the fry of salmon and trout is very strongly dominated by frontal attacks. As long as detailed studies of these movements are missing, their commonest pattern can only be approximately described as a darting approach concluded either by a threat bite (cf. p. 74) or by a real bite. In the former case the behaviour can be designated as nipping (HOAR 1951). The frequency of real bites in fry is, however, so high that the question might be raised whether or not many of the threat bites in reality are real bites which have missed their aim.

On a few occasions the fry was observed to approach the antagonist at comparatively slow speed. This took place with convex profile of the back and lowered dorsal fin, i.e. with the attitude which has been designated as frontal threat display. Also lateral threat displays occurred seldom. They were characterized by a very strong over-stretching of the vertabral column and general erection of the fins. Other possibly occurring elements escaped observation.

Already during the first weak the fry showed displacement feeding and prey-shaking after unsuccessful feeding excursions ("after-discharge of the feeding drive", FABRICIUS 1953 a).

In spite of the fact that threat signals were thus developed already upon a very early stage, they did not seem to play any more important rôle in the territorial fights before the fish had reached a length of at least 6--7 cms. The often extremely violent and protracted fights of the fry of salmon and trout were instead characterized by a great measure of raw aggressiveness in which visual signals were entirely subordinated to physical violence. From the earlier description of the conditions in the parr (p. 74) it appears that the parr of trout retain much of the behaviour pattern of the fry. In the salmon we can prove a development which leads to an almost complete replacement of the real fight by sham fighting by means of visual signals. Only in connection with the territorial fights upon the spawning grounds do real bites reappear in the salmon. During the spawning time fights between male salmon have been observed in the stream tank in the course of which one of the fishes kept hold for several minutes of a pectoral fin or the tail peduncle of the antagonist.

The observations in the aquarium point throughout to an intimate connection between feeding and aggressiveness in the fishes studied (cf. also p. 90). In the course of the development of the individual signs of aggressiveness are noticed only after the young fry has started to feed. As an evolutionary factor the fixed station implies that the fish takes advantage of the continuous conveyance of food with the current in a way which saves its energy. The aggressiveness of the juvenile salmon and trout becomes phylogenetically comprehensible only if it is conceived as a continued evolution connected with the feeding behaviour. The defence of the stations with the surrounding areas, i.e. the establishment of territories leads to a spreading of the population and to a more efficient utilization of the food supply. Together with the territoriality the strongly specialized feeding behaviour forms a complex which in a lotic environment must be considered to possess an obvious survival value.

VI. The Territoriality-Schooling Transformation

In the course of his investigations into the behaviour of the fry of salmon and sea trout carried out in the stream tank of the Salmon Research Laboratory LINDROTH (1956) found that the fry left the bottom, when the velocity of the current was lowered towards zero. They now stayed in the open water, where they swam to and fro in the aquarium. This observation has been confirmed several times in the course of work with the stream tank.

In July 1955 experiments were carried out with the aim of throwing more light upon the connection between velocity of current and territorial behaviour. The stream tank contained 54 salmon fry of about 40 mms.' length all of which occupied stable territories. The depth of the water was kept at

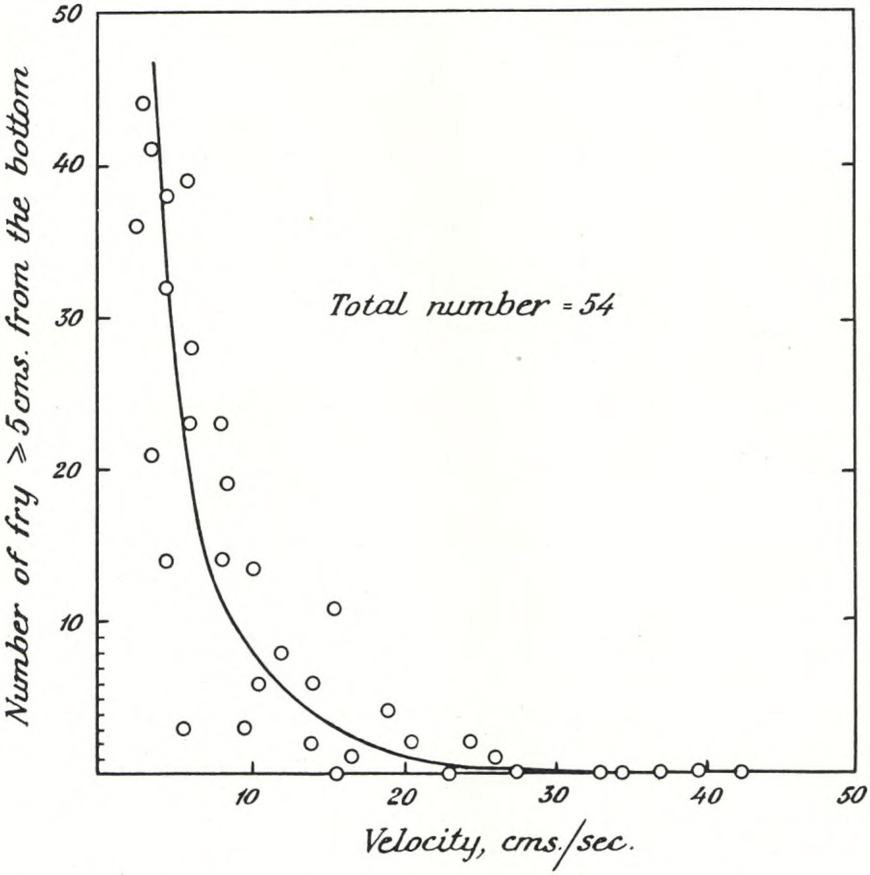

Fig. 10. Number of salmon fry in free water in relation to velocity of current.

25—30 cms. above the level of the gravel. In midstream the velocity of the current, determined as the average velocity in the uppermost 20 cms. of the water, was at the beginning of the experiments 42.5, 39.5, 33.0, and 24.5 cms./sec., respectively. In each of the experiments the velocity was lowered by 5—10 cms./sec. with intervals of 60 minutes. Immediately before each lowering the number of fry at a distance of at least 5 cms. from a solid surface was counted during a period of 15 minutes. When in this way the velocity of the current had been lowered to less than 5 cms./sec., it was raised again in the course of a couple of hours, and maintained at a constant level until, two days later, the next experiment was started. During this time the fry regained as a rule their particular territories. The results of the four experiments have been collected in Fig. 10 in which every dot signifies an average value of 10 counts during a period of 15 minutes. The diagram illustrates the strong dependence of the behaviour of the salmon fry upon the conditions of current. In the interval between the velocities of 10 and 5 cms./sec. the fry left their stations at a considerably increased rate.

The reactions of juvenile salmon and trout to current make it obvious that for the time being a sceptical attitude is indicated towards conclusions about the behaviour of stream fishes, if these observations have been carried out in aquaria of the common type. It was probably on account of the absence of current that STUART (1953) has found in salmon fry "all signs of a gregarious nature". But it is not admissible, on the other hand, to assume territoriality in a fish, when living in lakes, for the mere reason that this behaviour has been observed in the same species in running water.

The experiments described so far were interrupted as soon as the majority of the fry had left their stations. In other experiments in which the velocity of the current was lowered in the course of two hours from the normal 18—25 cms./sec. to almost zero the events in the aquarium were kept under observation even after the lowest velocity of the current had been reached.

When with decreasing current the salmon fry left the bottom, they stayed to start with close above their stations, swimming against the current. Subsequently the fry spread in vertical direction through the entire mass of water. On the fry approaching each other too closely a certain feeble aggressiveness, as sporadic nipping, was observed. Since the fry, after their brief feeding excursions, always returned to their places, it might be justified to speak upon this stage about stations in the open water.

When the velocity of the current had dropped almost to zero, the picture was increasingly influenced by a new element, consisting in a very slow up-stream migration of the fry in the aquarium. In order to establish this migration in the experiments the fry in each of the five sections of the aquarium were counted every four minutes, beginning from the moment, when the smallest velocity (1—2 cms./sec.) had been reached. Fig. 11 sums up the results of a typical experiment, showing a continuous decrease in the number of individuals in section V, the down-stream section. After 16 minutes all fry have left the section. In the three intermediate sections the number of individuals remains at first constant. Before the evacuation of section III a feeble maximum is indicated in it. This maximum is very pronounced in section II. In section I, the up-stream section, the number of individuals increases after a sigmoid curve, until after 36 minutes all fry in the aquarium are assembled in this section.

Superficially the movements of the fish during the experiment appear to be only a slow up-stream migration. A closer examination of the distribution of the experimental fishes in the different sections of the aquarium showed nevertheless that the migration as such is not the essential feature of what takes place. The maximum of the number of individuals in the intermediate sections can thus be explained only if the process is viewed as a gradually

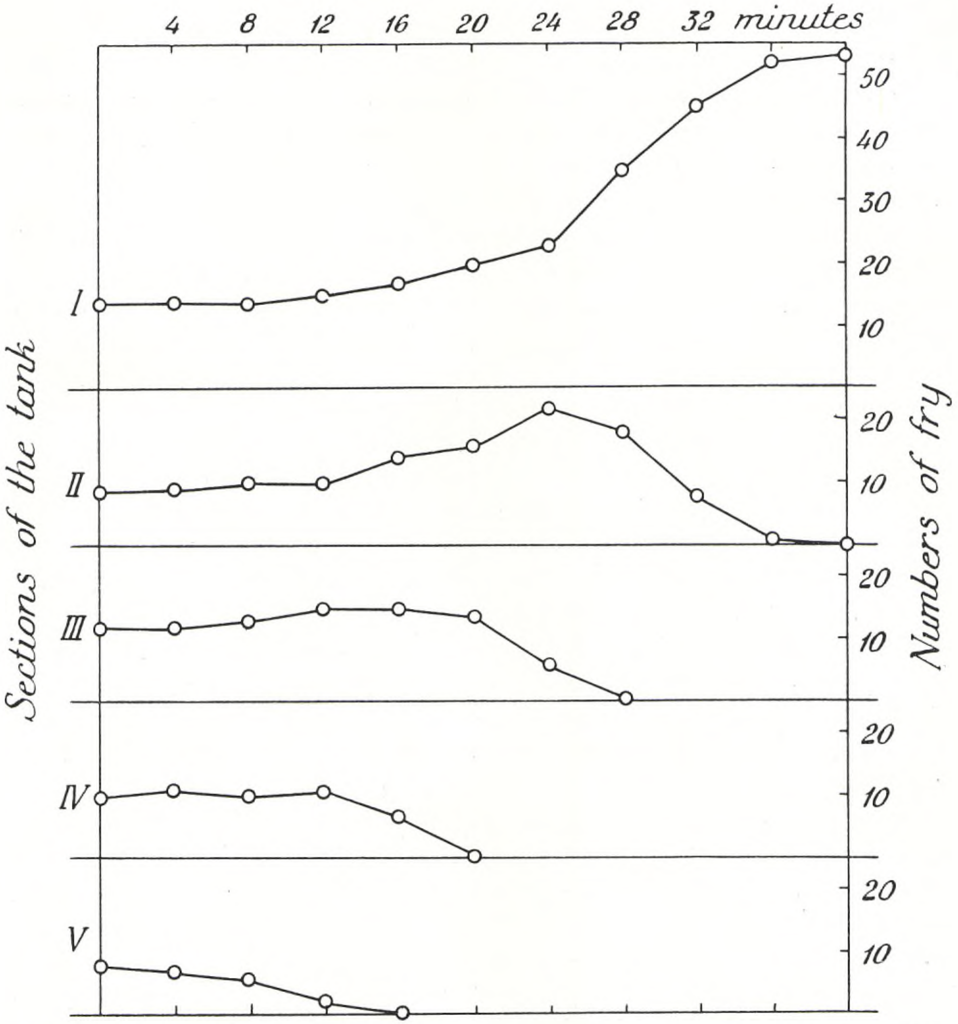

Fig. 11. Variation in number of salmon fry in each of the five sections of the stream tank after that the velocity of current had been lowered to almost zero. I=upstream section.

progressing contraction of the entire population. If, however, this contraction took place in a rectilinear fashion, i.e. if each of the fish migrated upstream with constant velocity until it had reached the uppermost section, the ascending branch of the curve would be concave, the maximum a point, and the descending branch of the curve convex. The sigmoid course of the branches of the curve reappeared, however, as a distinct tendency in all experiments, and can be explained only by the assumption that the velocity of the up-stream swimming in the different individuals in the aquarium varies with a sigmoidal function of time. As in the final stage the contraction takes place at a slower and slower rate, the reason might be found in the aggressiveness between the individuals which becomes more pronounced with the decreasing mutual distance. Such an interaction of attraction and repulsion between individuals is known from studies about the structure of the fish school (cf. BREDER, 1954, and the references given in this work).

Already during the up-stream migration of the fry local tendencies towards schooling were noticed here and there: When any of the fry deviated in a lateral direction its neighbours followed suite.

As the sluice gate of the aquarium was not entirely watertight, the velocity of the current could normally not be lowered to zero. In the very feeble remaining current the fry all the time exhibited "positive rheotaxis". This orientation, in combination with the reasonable assumption that the fish more easily observed objects directly in front of it than behind it, can explain the fact that in all experiments the contraction took place in the direction against the current. KEENLEYSIDE (1955) has shown that an isolated fish with the choice between two schools always joins that from which it receives the stronger visual impression. When in a couple of experiments by means of different makeshift arrangements, the current of the water in the aquarium had actually been reduced to zero, the school afterwards left the upstream section, and cruised to and fro in the aquarium in order now and then to come to a standstill, milling. As soon as the fry were frightened the distance between the individuals immediately diminished.

During one of the last referred experiments salmon fry were kept in quiet water for 46 hours. In the course of the second day the school started to dissolve. Tendencies towards schooling behaviour still remained, but by staying for shorter periods in the same place of the aquarium, and by chasing away intruders an increasing number of the fry reverted to a kind of partial territorial behaviour. Only when the fish had been violently frightened, e.g. by stirring up the water with a hoop net, the school collected again after an initial scattering of the fry in all directions.

It was demonstrated by HOAR (1951) that juvenile coho salmon (*Oncorhynchus kisutch*) are territorial, and that their aggressiveness decreases significantly during smoltification. In this respect I have no quantitative information for the Atlantic salmon, but numerous observations accumulated during the work described in these pages suggest that also this species might exhibit a decreasing aggressiveness prior to the down-stream migration.

For the investigations into the course of the smolt migration use was made, amongst others, of a circular channel with an outer diameter of 15 ms. and a width of 2 ms. During the culmination of the smolt migration the fish actively swam day and night in this channel with the current. The migration could continue for weeks, interrupted only by the feeding of the fish. All the time the smolt exhibited a pronounced schooling behaviour. (A full report on these investigations will be given in a paper now in preparation).

On being transferred into the stream tank actively migrating smolt immediately drifted or swam down-stream. After heading against the current at the down-stream grating for one or a couple of hours the fish exhibited aggressiveness, and spread, close to the bottom, in up-stream direction. During the following hours violent territorial combats were observed, but already on the following day stations had been established. Thus the smolts reacted upon the transfer into the aquarium in exactly the same way as parr of salmon and trout. Smolts were kept in the aquarium all the time, while the migration took place in the circular channel. When, later in the summer, the smolt transformation of the fish in the channel retrograded in part (parr marks appeared again, blood sugar values dropped, and liver glycogen values rose), corresponding changes were observed in the stream tank in the territorial smolt.

If during the period of migration territorial smolts from the stream tank were retransferred to the circular channel, they started within in few hours their active migration as if they had never done anything else. If, on the occasion of the transfer the circular channel already contained migrating smolts, the newcomers usually joined the school after having stayed at the bottom for only a few minutes.

The observations reported here produce a strong impression as if in the juvenile salmon two essentially opposite reactions between individuals weighed against each other. In fry and parr the point of equilibrium is displaced for the benefit of aggressiveness and territorial behaviour, which become altogether dominant. In migrating smolts schooling is the normal reaction. Only if the velocity of the current is sufficient, does the aggressiveness express itself a complete territoriality. When the velocity is lowered towards zero schooling tendencies become evident also in fry and parr. In the migrating smolt the aggressiveness seems to be suppressed by a, then stronger drive for schooling. If the migration is prevented by purely mechanical means the smolt reacts by immediately switching over to the other of the alternative behaviours. The reactions of the smolt nicely exemplify the general rule of inhibition between instinctive activities of the same level (cf. TINBERGEN 1951).

VII. Competition

A. *Introduction*

In an important paper LARKIN (1956) shows that the term competition, by being linked to the conception of niche ("competition for a niche"), has obtained an amplification which under natural conditions appears unrealistic. LARKIN proposes the restriction of the term in accordance with DARWIN's original definition in "The Origin of Species" to the demand of more than one organism for the same resources of the environment in excess of immediate supply. Only by this feature, LARKIN maintains, does the competition become a discrete phenomenon which "can be measured as a factor involved in interaction between species".

In the majority of investigations into this matter the attempt has been made of directly approaching the competition for food. It is, however, remarkable how difficult it has been to ascertain unambiguous competition by examinations of the choice of food. Competition for food is conditioned by the fact that the supply of food is at a minimum — "the fact that different species of fish eat the same foods is not just cause for assuming they are competing" (LARKIN 1956). Plasticity in the food habits seems also to enable populations of fish to change diet "rather than enter into severe competition" (STARRET 1950).

While the course of the direct competition for food of fishes appears as a rule obscure, the competition for space, where it manifests itself as territoriality, offers a clearer picture. Here the expressions of aggressivity are accessible to study by ethological methods. This way of attacking the problem appears promising, but has been entered upon only in the course of the last years (NEWMAN 1956, cf. also KING 1957).

B. *Intraspecific competition*

Within populations of juvenile salmon and trout the competition for space depends partly upon the potential aggressiveness of the individuals and partly upon external factors, especially the population density, i.e. the available space, and the degree of visual isolation within the biotope. These determine to what extent this aggressiveness can express itself as competition within the population. From among the external factors the importance of visual isolation has already been pointed out (p. 65). Here we shall account for the way in which the population density made itself felt in captivity, when a varying number of salmon fry (O-group) reared in troughs was kept in the aquarium.

When the number of individuals was very small (about 20 fry) all individuals defended territories, the stations being far distant from each other. After the stabilization of the conditions even an observation through hours of the fishes often did not reveal a single act of aggressiveness within the population. If a greater number of fry was introduced into the aquarium the aggressiveness became increasingly noticeable. Up to a total number of 200 to 250 individuals all fry occupied, however, normal territories, i.e. the size of the territories changed in direct proportion to the population density. The mentioned number of fry corresponds to an average size of the units in the territorial mosaic of 2.7—3.4 sq.dms. In the aquarium this density appeared

Fig. 12. Salmon smolts actively migrating downstream at experimental conditions.

to constitute a critical limit. If it was exceeded, the population split in a very striking way into two fractions. One of them consisted of 200—250 dominating individuals occupying territories of the critical average size. The other fraction was formed of individuals which where chased from place to place in the aquarium, unless they kept quietly in the fissures or defended minute territories in holes between the stones of the bottom. In such holes which often were not larger than a walnut, and where normal feeding was of course impossible, violent contests were often fought, when one of the chased fry without territory happened to enter the hole. The entire population was characterized by a striking instability. There occurred a certain circulation between groups consisting of individuals with and without territories. This exchange can, however, not have been very great, since the observation has always been made that in the case of high population density a noticeable difference in size between the two fractions is developed in a few weeks. The splitting into individuals with and without territory has been made use of for observations as to how increased velocity of current or increased turbidity reduced the critical size of the territories by increasing the visual isolation of the individuals (p. 66).

In the course of intensive rearing of territorial salmonids population densities occur which have no counterpart under natural conditions. Every pisciculturist knows that in the rearing troughs the fry do not as a rule exhibit any territoriality. Instead of it more or less distinct tendencies towards schooling are observed. If this effect were merely a consequence of the population density at a given time, the aggressiveness ought to manifest itselft as soon as the fishes are given more space. This has, however, not been the case, and in the stream tank salmon parr were slower in exhibiting aggressiveness the longer they had previously been exposed to the influence of over-crowding. Neither is it possible to look for the causes in the general artificial environment, since fishes which had lived for a longer time in extremely sparsely stocked troughs almost immediately exhibited aggressiveness, when transferred into the stream tank. The effect of over-crowding must be interpreted as a more or less durable and severe blocking, due to the continuous contact for some time between individuals, of the nervous mechanisms lying behind aggressive behaviour.

Under natural conditions it is probably not normal that, as in the abovementioned experiments, the competition within a population of fry of salmon or brown trout becomes intensified by an increase in the number of individuals, but rather by the growth of the individuals. A larger fish has on the average a greater potential aggressiveness than a smaller one, and *ceteris paribus* asserts himself within a larger territory (p. 65). In the stream tank it has repeatedly been observed that fry which at an early moment had conquered good stations (exposed, near the grating for the entering water, etc.) grew noticeably faster in the continuation. The frequency of aggressive contacts was on the other hand greatest at the times, when the fish fed most intensively, i.e. in the mornings and evenings (p. 71). NEWMAN (1956) had found the aggressiveness of his experimental fishes to increase during artificial feeding. In the stream tank it could occasionally be difficult to decide, whether a certain fish kept a territory or not, provided the fish did not show any hostility against intruders. In such cases aggressive behaviour could be induced by artificial feeding. Usually after only one or two feeding excursions the fish immediately attacked an intruding neighbour. This reaction of a single fish may indicate that the increased aggressiveness during feeding is not exclusively due to the fact that on such occasions the individuals come into closer proximity.

The mutual linkage between feeding and potential aggressiveness must lead to a fast increase of the differences of size within the population. A fish which just by means of his aggressiveness has succeeded to conquer a station with favourable feeding conditions finds it less difficult to maintain itself in possession, partly on account of the stimulation of the aggressiveness during the intensive feeding, partly by the fact that it grows faster than its neighbours with less advantageous stations.

If it shall be possible in the aquarium to follow the development of the territorial mosaic during the growth of the individuals, the mosaic has to be small in comparison with the bottom area of the aquarium, at least at the start. For this reason two groups of about 50 each of hatching salmon eggs were deposited in the stream tank at a distance of about 5 ms. from each other. Within 3—4 days from the hatching the alevins disappeared into the gravel. After the resorption of the yolk sac the fry of each group emerged from the gravel within an area of about 25 sq.dms. About a week later they had spread by means of their movements, mainly downstream, so that each group now covered approximately twice that surface. Simultaneously they had occupied stations, i.e. a first territorial mosaic had been formed in which the units covered on the average about 1.1 sq.dm. After a further month the mosaics covered the entire width of the aquarium, to a length of about 1.4 and 1.6 metres, respectively, (average size of territories about 3.1 and 2.9 sq.dms., respectively). In addition a number of fry occurred isolated outside the mosaics. Individual differences in the pigmentation have made it possible to follow the movements of fry near the glass during the expansion of the mosaic. The fry could be observed by steps to carry out small movements of the stations, but the expansion was effected only, when the fry made sudden moves over longer distances. A fry which had been under observation for several days could disappear from its customary place, but was often rediscovered in the periphery of the mosaic, where it now defended a new territory. This emigration and renewed colonization could be directly observed, when one of the parties fled after violent fights.

Already in an early phase after the emergence from the gravel the fry might be spread by a mechanism which is entirely different from the aggressiveness. Since the days of VOGT (1842) the statement is met that fry of salmon and trout for the first time fill their swimming bladder by snapping after air at the surface. With the ordinary conditions in the aquarium this conception is certainly correct. Fry with still empty swimming bladder swim in the open water with noticeable difficulty, and are on this account easily recognized. In the stream tank fry were occasionally noticed to ascend to the surface, where also the snapping after air could be observed. These fry swam, however, unimpeded, and already kept fixed stations. A check by means of examining the fry in transmitted light showed moreover that also among the fry which still had not occupied stations a considerable fraction (6 out of 15 examined individuals) had already a filled swimming bladder. If the fry makes excursions to the surface of the water already upon this early stage, a very considerable spreading, mainly in down-stream direction, of the population must result under normal conditions of depth and current. No such early spreading could be established as can be gathered from the above description of the experiments in the stream tank. These facts can be explained only by the assumption that in the stream tank the fry of salmon and trout fill their swimming bladder already at the bottom. This assumption is supported by observations of the behaviour of young fry. Their feeding proved to be very unspecific: all moveable objects of suitable size, amongst them small air bubbles, were caught in the current (p. 81).

The observations in the aquarium make possible a hypothetical conception of the dynamics of the territorial mosaic. Each territory in the mosaic is maintained by the aggressiveness of the defender which can roughly be compared with a pressure decreasing from the station towards the periphery. The actual position of every boundary between the territories within the mosaic is such that the pressures on either side of the boundary are equal. If the potential aggressiveness increases, e.g. through the growth of the individuals, the mosaic as a whole can expand uniformly in a small degree only, since its pattern is fixed by the stations. Instead of it the "pressure" (i.e. the competition for space) within the mosaic increases, the boundaries between the territories being shifted at the same time in relation to the differences in the growth of the individuals. Since thus the area of the territorial mosaic is only inconsiderably widened (through smaller moves of the stations in centrifugal direction), the absolute average size of the territories remains almost unchanged, while the relative size decreases continuously in order finally to become critical in relation to the aggressiveness. When this happens, the mosaic starts to break up. In our physical parlance this can be said to happen by the crushing of the "walls" of the most feebly defended territories. The fry which as the result of the competition for space have lost their territories take to flight, and arrive outside the original mosaic. They then occupy new territories. In this way the territorial mosaic expands over an increasingly growing area, yet not through a uniform magnification of the original pattern, but through disrupture and reconstruction. In the mosaic the abrupt course of events in the individual territory manifests itself as a higher frequency of aggressive contact and by an on the average lower stability of the stations, when the specific growth rate is high.

Observations in the field show fights for territories to be common under natural conditions (NEWMAN 1956). The assumption appears reasonable that there exists a permanent lack of suitable space with regard to the size of the growing populations. A considerable number of the fry which by the competition within the mosaic have been forced to relinquish their territories will thus probably have to be satisfied with stations which from the point of view of food supply are inferior. On this account the competition for space becomes, as in the aquarium, also a competition for food. The slow-growing individuals are eliminated to a greater extent from the population, since they remain for a greater length of time within the size group which runs the greatest risk from predation. This increased risk from predation brought about by retardation of growth has been considered by LARKIN (1956) as one of the most important consequences of intra- and interspecific competition in communities of freshwater fishes. Since the intensity of the competition is thus *inter alia* a function of the growth rate of the individuals, it ought to make itself felt first of all in populations of young individuals with high specific growth rate.

C. *Interspecific competition*

The aggressiveness of territorial salmonids is probably released by very simple visual stimuli of the type "moveable object of moderate size". In the foregoing it has been mentioned (p. 68) that territorial salmon fry attacked the point of a stick, and FABRICIUS and GUSTAFSON (1955) found grayling to "attack" a photometer which was moved to and fro outside the spawning aquarium. In the stream tank the juvenile salmon and trout exhibited aggressiveness against every fish, irrespective of kind, which was not considerably larger, and which approached the station (salmon, brown trout, minnow, roach, perch) (cf. also LINDROTH 1956). These observations are clearly in variance with the conditions in *Serranus scriba,* which usually defends its territory only against individuals of its own species (KIRCHSHOFER 1954). Essential differences could, however, be observed in the reactions of different intruders in the face of the threat by parr of salmon or brown trout. A minnow thus yielded to severe aggressiveness, e.g. threatening approach, threatening bites, but did not react to lateral display more than to any movement carried out by a fish in the neighbourhood. The relations between the parr of salmon and brown trout assumed quite a different aspect. As described above the threat displays of the two species are qualitatively very similar, i.e. composed of the same basic elements. In mixed populations the sham fights were entirely independent of the species involved, and there existed not the slightest reason for doubting that the parr of salmon and brown trout mutually understood their threat signals. The same seems to hold good for the relations between brook trout (*Salvelinus fontinalis*) and rainbow trout (*Salmo gairdneri*). As the result of field studies of these species NEWMAN (1956) says that "they behaved toward each other as though they were one species".

The parr of salmon and brown trout thus possess for their aggressive purposes an interspecifically understandable means of expression. And since at the same time the biotopes for their early development in a large measure overlap in nature, the necessary conditions for the carrying on of the competition between the two species on the behaviour level are given.

There is good reason for supposing with LINDROTH (1956) that in this competition the parr of salmon are having the worst of it. Almost every element of the threat displays is carried to greater intensity in the parr of the brown trout than in that of the salmon. This implies a corresponding increase of the threatening value of the complex signals. To this must be added that the trout parr avails himself to a larger extent of stronger means of expres-

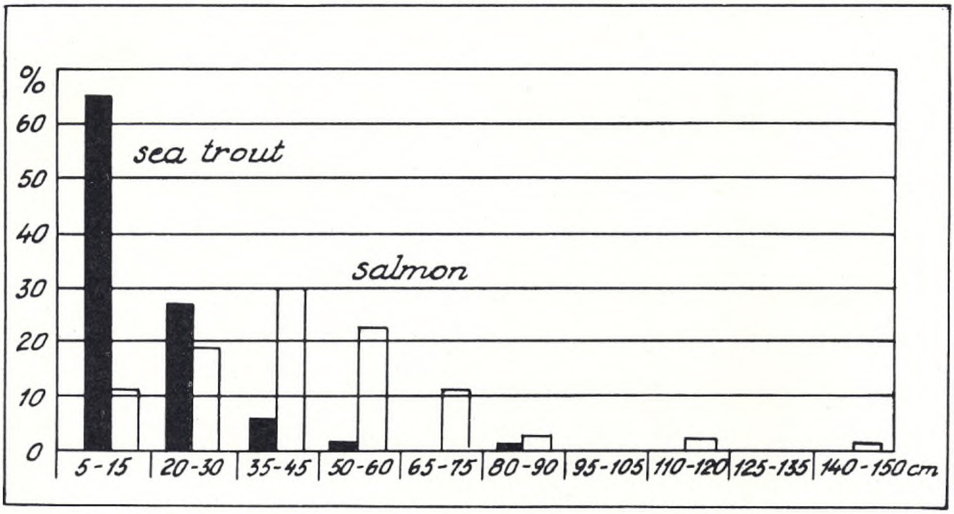

Fig. 13. Vertical distribution of salmon and trout yearlings in Indalsälven. From LINDROTH (1956).

sion, the sham bites of the salmon parr being met by real bites. All observations in connection with aggressive contacts of the two species in the stream tank point to a clear dominance of the trout parr over a salmon parr of about the same size. On account of the faster growth of the brown trout this dominance can be expected to be still more pronounced in the field.

LINDROTH (1956) studied the vertical distribution of the parr of salmon and sea trout in Indalsälven, Sweden, and presented the collected results in a diagram (Fig. 13). This shows the population density of the trout to increase continuously and at a fast rate towards the beach, whereas the greatest density of the salmon population was found at the depth of about 45 centimetres. In the Norwegian Oselva, on the other hand, which is an almost exclusive salmon water parr of salmon were encountered "in localities quite comparable, ecologically, as far as could be judged to those in the Indalsälven where the trout fry are found". LINDROTH supplies no information about the lengths of the fishes which form the basis of his diagram. On account of their faster growth the trout parr ought, however, to have been larger on the average than the parr of salmon. This makes the distribution in the Indalsälven appear still more remarkable, since on the basis of experience one should expect to find larger fish at greater depth. LINDROTH concluded that we had to do here with "a typical case of competition possibly with a tendency to amensalism".

It is known that populations of closely related, allopatrically living species can have closely situated ecological optima, and that in this case intraspecific competition alone can compel each of the species to utilize all its ecological

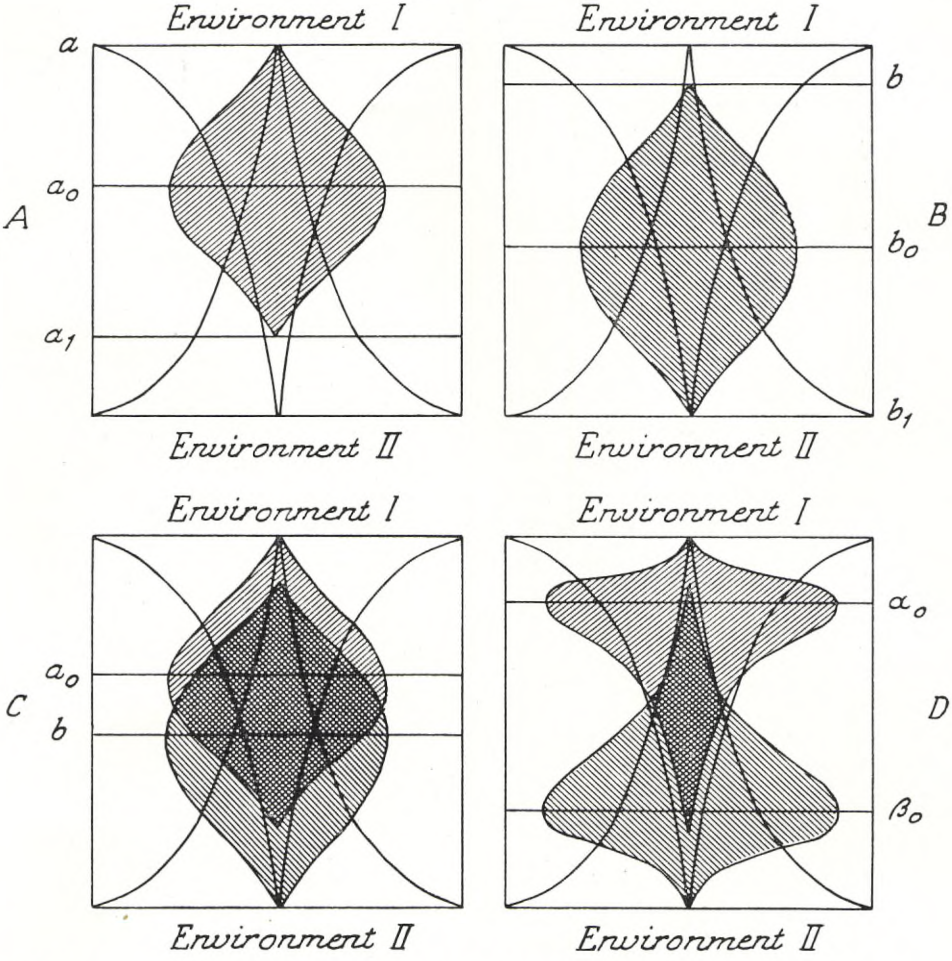

Fig. 14 A and B: Two closely related species living allopatrically, a—a_1=ecological potency of species A, a_0=optimum of species A, etc. C: Two closely related species living sympatrically in a temporary superabundance of ecological resources. D: Two closely related species living sympatrically in competition, α_0 and β_0=new optima of species A and B, respectively. From NILSSON (1956).

potency. If, on the other hand, the populations live sympatrically, though under interspecific competition, the optima are removed from each other, while at the same time the amplitudes around these new optima become narrower (SVÄRDSON 1949, NILSSON 1955, 1956; Fig. 14). In spite of the fact that we have no quantitative, entirely comparable data for the vertical distribution of the parr of salmon and brown trout, if the species live allopatrically, it appears not very probable that under such conditions the "depth optima" could be as well separated as in the Indalsälven, where the species live sympatrically. It appears obvious that the interesting distribution of the parr of salmon and sea trout in the Indalsälven is the result of interspecific competition, and observations in the aquarium of the ethology of the species show that in all probability the trout dominates in this competition for space.

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Observations sur les cycles annuels des planctons crustacés
Dualisme des populations Copépodes — Répercussion des années froides — Differences entre des lacs

Par THOROLF LINDSTRÖM

Table des matières

Introduction

Les populations de planctons crustacés sont stables dans de grands lacs, selon HUITFELT KAAS (1946 posthume) et BALDI (1951), en ce sens qu'elles parcourent les mêmes cycles annuels, années après années, et retrouvent entre elles les mêmes relations quantitatives. D'après ces deux auteurs la stabilité des populations de planctons des grands lacs est dépendante de la stabilité du milieu. On cite aussi dans ces deux ouvrages et dans les travaux de WAUTIER (1951) et D'ANCONA (1955), certains travaux dans lesquels on parle de changements qui ont eu lieu dans la composition des planctons crustacés. Cf. aussi FINDENEGG (1935), PENNAK (1946, 1949), TONOLLI (1954), WOLF (1955) et RAWSON (1956).

De telles modifications n'ont rien de surprenant lorsque l'on a la çertitude que le milieu a subit des changements radicaux (D'ANCONA 1941, RICKER 1937, 1938, et ELSTER 1955).

Dans une étude précédante, en 1952, p. 113, j'ai présumé une certaine stabilité dans les populations de planctons crustacés des lacs du Jämtland que j'avais étudiés, obtenant ainsi le groupement suivant: a) lac pauvre en planctons et à fort courant, Gesten — b) lacs riches en Cladocères, Hottön et Håckren — c) lac très agité par l'effet des vents, Ottsjön, dont la population en Cladocères est d'une importance moyenne, mais possède une population de Copépodes bien plus importante qu'en aucun des autres lacs.

Dans une étude plus récente (1957) des indices avaient été rassemblés qui faisaient penser que les *Bosmina* étaient mieux adaptés pour vivre dans une eau courante que les autres planctons crustacés que nous avions traités. Il ressort aussi dans les graphiques 11—12 de la présente étude que, dans le Gesten, la population de *Bosmina* n'est pas spécialement pauvre.

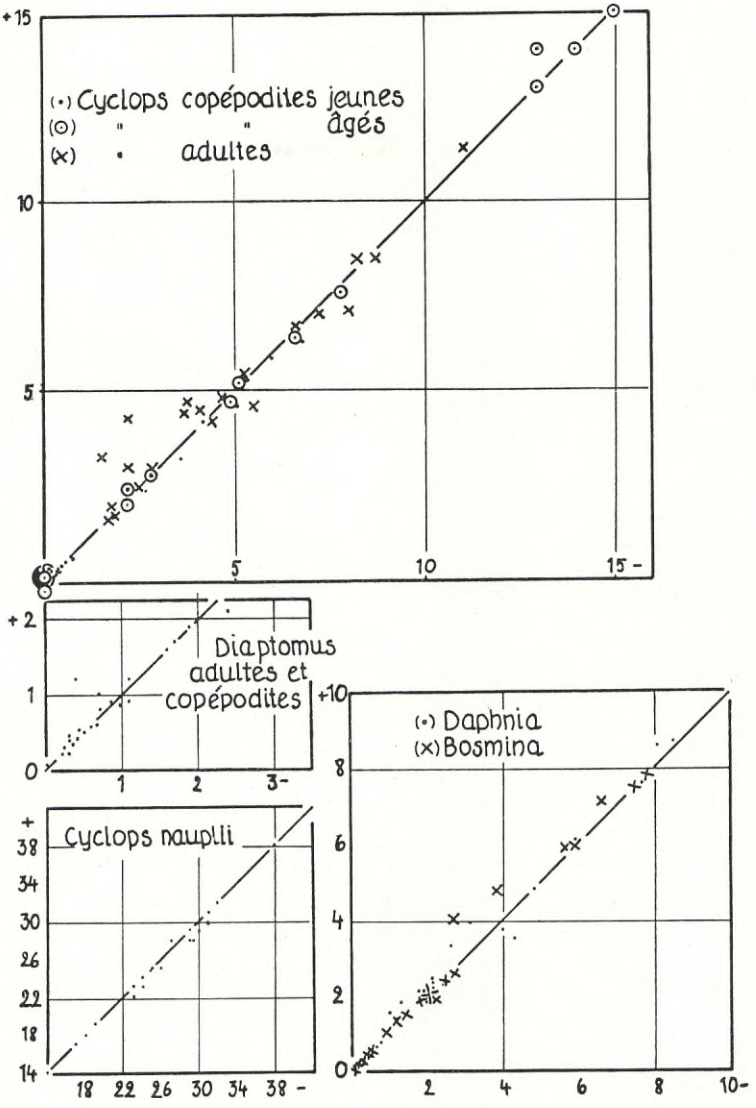
Du nouveau matériel a été rassemblé qui permet d'étudier le cycle annuel des planctons crustacés et la différence entre les lacs mentionnés. Une question retiendra plus spécialement notre attention, à savoir, si la différence de température entre les années peut avoir un effet mesurable sur les populations.

Systématique et Méthode

A ce qui a été dit au sujet de la systématique, dans le précédent travail (1952), il faut ajouter ce qui suit:

La classification des *Cyclops* copépodites est plus détaillée qu'en 1952. Des copépodites *Heterocope saliens* LILLJEBORG et des copépodites *Diaptomus laticeps* SARS ont été complètement séparés à l'aide des travaux de GRANDORI (1912) et de RAVERA (1953). Les *Daphnia* ont un ocelle pigmenté et n'ont pas de peigne sur la griffe terminale de leur postabdomen. Les *Daphnia* à tête ronde du printemps et du début de l'été n'ont pu être classifiés avec certitude, en prenant comme référence la mesure de la lisière située entre la pointe du museau et le sommet de la tête, ni comme *Daphnia longispina hyalina* LEYDIG, ni comme *Daphnia longispina longispina* O. F. MÜLLER (LILLJEBORG 1900, Fig. XIII: 3 et XVI: 5). On peut présumer que la population consiste seulement en *Daphnia longispina hyalina* car avant que les dernières femelles à tête ronde aient disparu au milieu de juillet, il n'a été trouvé aucun mâle dans Håckren et très peu dans les autres lacs et seulement un éphippié (libéré), et les mâles — qui paraissent plus tard — sont munis d'une épine à la carène.

Les moyennes de densité dans des colonnes verticales pour les planctons crustacés, qui sont reproduites dans les Graph. 2—4, 6—9, 11—12 ont été construites de la façon suivante: Tous les chiffres initiaux ont été recalculés sur une base de cinq litres. De plus on donne plus ou moins de poids aux épreuves prises à différentes profondeurs afin que les épreuves de surface et les épreuves prises à 2 m. de profondeur, quand ces dernières existent, fournissent une caractéristique d'une région de 1 m. et d'une région de 2 m. dans la colonne verticale jusqu'à 3 m. de profondeur. Les épreuves prises près du fond fournissent ainsi une caractéristique des deux mètres les plus profonds de la colonne, pourvu que les épreuves prises près du fond ne le soient pas à plus de 2 m. du fond. Pour les autres épreuves plus la distance qui les sépare est grande, plus on leur a donné de poids. Cette façon méthodique de



Graphique 1. Densité moyenne dans la verticale, calculée avec (+) et sans (—) épreuves prises à deux mètres de la surface. Chaque signe se réfère à une série d'épreuves prises entre le fond et la surface. Les épreuves ont été prises du 4.7 au 30.8, 1950 et du 11.8 au 20.8, 1951, dans Ottsjön.

calcul est sans doute un peu arbitraire, mais vaut jusqu'à plus ample information. Les indications qui découlent du matériel suggèrent que la faible densité près de la surface et la forte densité près du fond existent sur étroite tranche horizontale du lac. Cela incline à donner moins de poids aux épreuves prises près de la surface et à celles prises près du fond.

Comme on n'a pas pris d'épreuves à 2 m. de profondeur au cours des premières années, ces épreuves sont aussi exclues de temps en temps des séries d'épreuves plus récentes. On trouvera les effets de cette méthode de travail dans les graphiques 1, 3, 4, 7, 8, 11 et 12.

Les densités moyennes calculées ne prétendent pas être de véritables densités moyennes. Le défaut de concordance entre les densités moyennes par épreuves de nuit et de jour est la meilleure illustration des imperfections inhérentes à la méthode. (Pour références consulter ULLYOTT 1939 et LINDSTRÖM 1952 p. 71, cf. aussi CLARKE 1934 b, GARDINER 1934, GROVER et COKER 1940.) Les auteurs des investigations marines indiquent qu'il arrive de temps en temps qu'on ne prenne pas d'épreuves de jour dans une région située près du fond et riche en plancton, (RUSSEL 1928, 1930, et GARDINER 1934, CLARKE 1934 b), cela suggère sans doute que pour les situations en eau douce les mouvements de fuite des planctons ne peuvent expliquer que partiellement les basses densités moyennes de jour.

Un essai d'estimation du vent a été fait pour Håckren en 1955, mais la force du vent n'a jamais été suffisante pour être relevée dans la discussion de la distribution verticale des planctons. Le vent n'ayant jamais dépassé un à deux mètres par seconde. De même la force du vent était faible lorsque les épreuves ont été prises dans Håckren en 1957.

La ressemblance qui existe entre les épreuves prises à la verticale avec filet entre le fond et la surface et celles prises avec le chercheur dans Håckren et Ottsjön en 1957 démontre la possibilité d'employer des épreuves prises à la verticale avec filet pour une recherche du cycle annuel (d'après une idée d'ELGMORK).

Nouvelles observations sur les Cycles annuels des populations

Les cycles annuels ont été traités lors d'une précédente étude, en 1952. A cette occasion les *Cyclops scutifer* et les *Diaptomus laticeps* ont été spécialement étudiés. Le matériel le plus important avait été pris dans Ottsjön, mais on avait aussi essayé d'établir une théorie valable pour une plus grande région et on avait donc employé les suggestions fournies par le matériel pris dans des lacs avoisinants.

Depuis un nouveau matériel a été pris surtout dans Håckren avec l'espoir de pouvoir valider ou d'invalider la théorie en l'appliquant à ce lac. (Des caractéristiques pour les lacs différents ont été données dans op. cit. 1952.)

La théorie établie en 1952 pour les cycles annuels des Copépodes impliquent que deux fractions existent dans les populations de *Cyclops scutifer* et *Diaptomus laticeps* et que leur cycles annuels suivent des rythmes différents. Déjà en 1918, OLOFSSON émettait une semblable interprétation (Cf. aussi WALTER 1922, COKER 1933, FILTEAU et TREMBLAY, 1952, WIBORG 1954 p. 97).

Ce dualisme n'était pas aussi apparent dans tous les lacs du Jämtland qui avaient été examinés (cf. AXELSON 1957). A l'aide du nouveau matériel on a pu vérifier l'absence d'une fraction de la population de *Diaptomus* dans Ottsjön. Dans cette fraction, les animaux sont copépodites pendant l'hiver, deviennent adultes et se propagent au printemps et au début de l'été. Par contre on a obtenu de nouveaux indices de l'existence de cette fraction dans d'autres lacs (Gesten, Tab. 1, 2 et 3 et Graph. 5).

Une partie des individus *Diaptomus* dans Hottön et Gesten (Graph. 2—4), et tous les individus dans Ottsjön et peut-être aussi dans Håckren appartiennent par contre à une autre fraction dans laquelle les individus sont éclos, des œufs durables, au printemps. La frontière entre les deux fractions n'est peut-être pas très bien déterminée dans Hottön et Gesten dans ce sens que les individus éclos d'œufs durables ne peuvent être distingués par la suite des enfants des adultes qui se propagent au printemps et au début de l'été. Mais il ne serait pas réaliste de nier qu'une certaine fraction provient des œufs durables.

Au cours du développement qui se poursuit après le printemps, le rythme est accéléré dans Ottsjön où les adultes se rencontrent déjà en juin, mais il ne se propagent pas avant le mois d'août. Dans Håckren et Hottön, le point culminant des copépodites n'arrive qu'en juillet et pour les adultes principalement en août et même éventuellement plus tard.

Le matériel de Håckren, à lui seul, n'a guère donné de motifs permettant d'établir la théorie du dualisme pour la population des *Cyclops*. Les observations peuvent donner à penser que la population au cours des six mois d'été, en général, a un potentiel de propagation, et, que ce potentiel donne naissance à une pulsation dans la population en mai—juin et en août—septembre, lorsque les conditions sont favorables. Cependant les observations faites au sujet de la population de *Cyclops* dans Håckren ne contrastent pas avec la théorie du dualisme dans la population des *Cyclops*: Le seul maximum de copépodites âgés qui a pu être observé dans Håckren peut très bien être complexe et contenir d'une part des copépodites réveillés de leur période d'engourdissement et qui sont remontés du fond et contenir d'autre part dans la partie estivale des individus développés de la pulsation de jeunes copépodites en juin, ce qui amène une conséquence correspondante chez les adultes.

La réserve qui sauve l'existence de la population durant les périodes critiques peut consister en copépodites âgés résistants à la disette et qui éventuellement reposent sur le fond (COLE 1955, FRYER et SMYLY 1954, ELGMORK 1955), en adultes isolés qui peuvent rapidement produire beaucoup d'œufs lorsque les conditions redeviennent favorables, ou enfin, des œufs que se sont développés très lentement.

Il est évident que ces trois groupes peuvent échapper à l'observation, soit parce qu'ils sont peu nombreux, soit parce qu'ils ne peuvent être pris par les chercheurs du fait qu'ils reposent sur le fond, ou encore à cause de leur petite taille. Ceci peut expliquer le manque apparent de nauplii à l'époque qui inclus la débacle de la glace si on compare avec la densité en jeunes copépodites durant la pulsation qui suit (voir plus loin), de même que le semblant de diminution de copépodites âgés en juillet 1955.

Un manque de nauplii et de copépodites âgés est d'ailleurs perceptible à la fin de l'hiver dans le matériel de Ottsjön. L'aspect d'hiver dans Ottsjön (nauplii et copépodites âgés, cf. AXELSON 1957) a été interprété dans op. cit. 1952, p. 102: «On peut préciser en disant que l'évolution des œufs et des nauplii est tardive en hiver, et qu'il est possible que les œufs produits par de très rares adultes, s'ajoutent de temps en temps au nombre de nauplii, de même qu'il est possible aussi que quelques nauplii se métamorphosent en copépodites en passant rapidement le stade copépodites jeunes». Il est facile d'expliquer, en se basant sur le résultat expérimental de COKER (1933), qu'un rassemblement de copépodites âgés se produit et que ces animaux donnent naissance à la fraction B de *Cyclops.*

Moins évident est la raison d'un rassemblement de nauplii durant l'hiver et comment se produit la fraction A de *Cyclops* qui existe dans tous les lacs. Des œufs durables n'ont pas été trouvés chez les *Cyclops.* Il manque de preuves expérimentales pour soutenir l'hypothèse de nauplii fonctionnant au stade de repos (EKMAN 1904, p. 101), mais la possibilité existe. Le manque de nauplii en hiver et au printemps et qui a été discuté dans le paragraphe précédent, demande en tout cas un complément d'explication: Conformément au texte de 1952, cité précédemment, il devrait y avoir une continuité dans la production de nauplii durant l'hiver. Quelquefois, probablement lorsqu'il y a une augmentation fortuite de la provision de nourriture, il y a une continuation de l'ontogenèse sur une plus grande échelle que celle indiquée dans la citation, car de jeunes copépodites ont été trouvés dans les épreuves de

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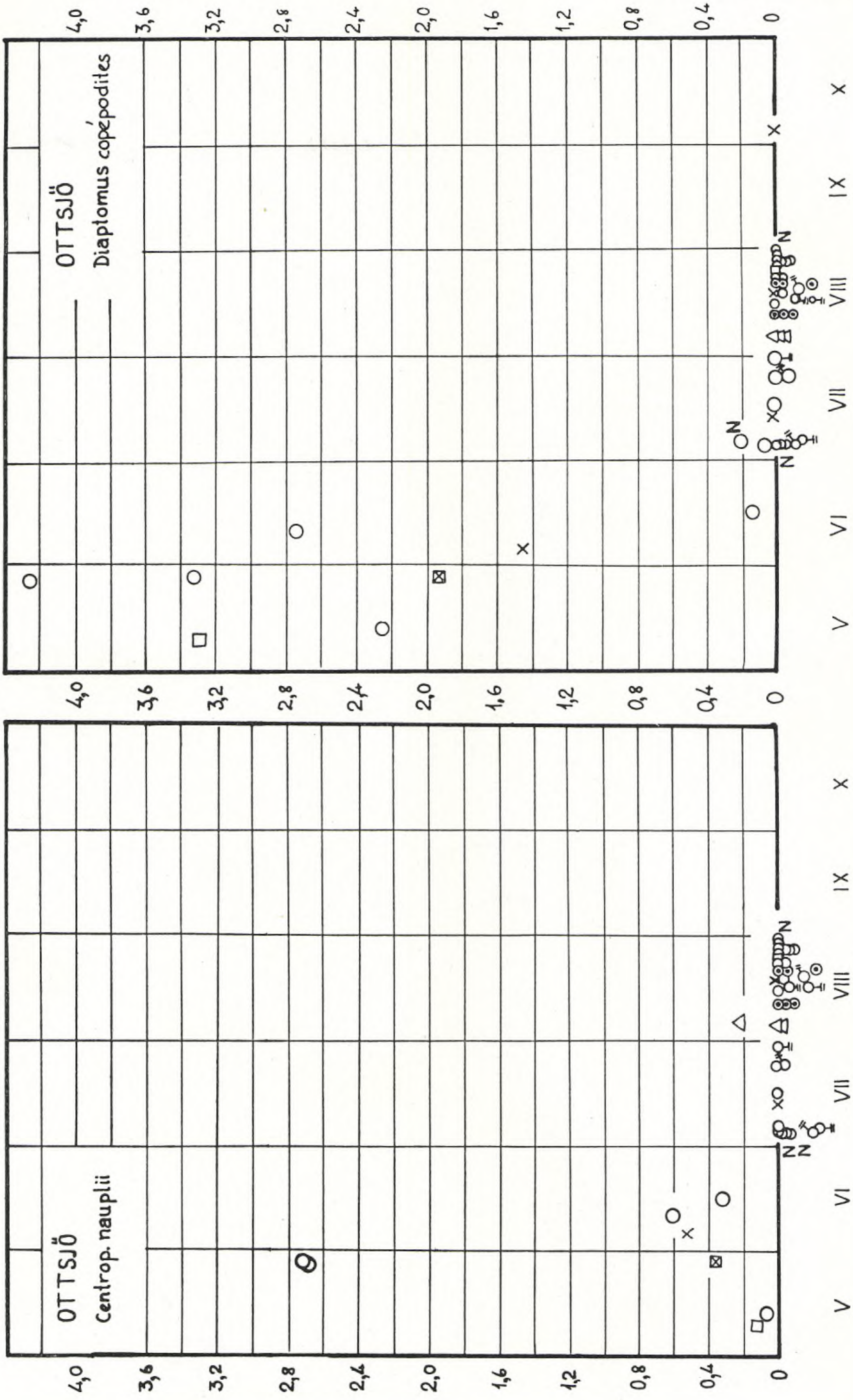
Graphiques 2—4. Densité moyenne par cinq litres dans une colonne verticale pour les *Diaptomus laticeps,* SARS. Epreuves prises avec chercheur de planctons. Rythme divergent dans Ottsjön. Des indices d'existence des deux fractions ne se trouvent que dans Gesten et Hottön.

Le matériel de ces graphiques et des graphiques 5—12 se trouve en partie dans le travail de 1952, tableau 9, et en partie dans le présent travail, tableau 2 et 3. Il est bon d'observer que deux échelles différentes ont été employées pour les épreuves de chercheur de planctons, et deux échelles différentes pour les épreuves de filet à la verticale. Les mois ont été indiqués, sous le graphique, avec des chiffres romains. Des épreuves de nuit sont indiquées par (N). Les épreuves à 2 mètres de profondeur n'ont pas été comptées dans l'établissement du graphique sur le chercheur de planctons, pour Ottsjön, mais par contre, dans toutes les séries d'épreuves, pour Håckren. Pour Hottön et Gesten on a établi des signes sans employer d'épreuves de 2 mètres pour toutes les séries; lorsque des épreuves de 2 mètres existent on a ajouté des signes établis à l'aide de ces épreuves et on a indiqué leur rapport avec les premiers.

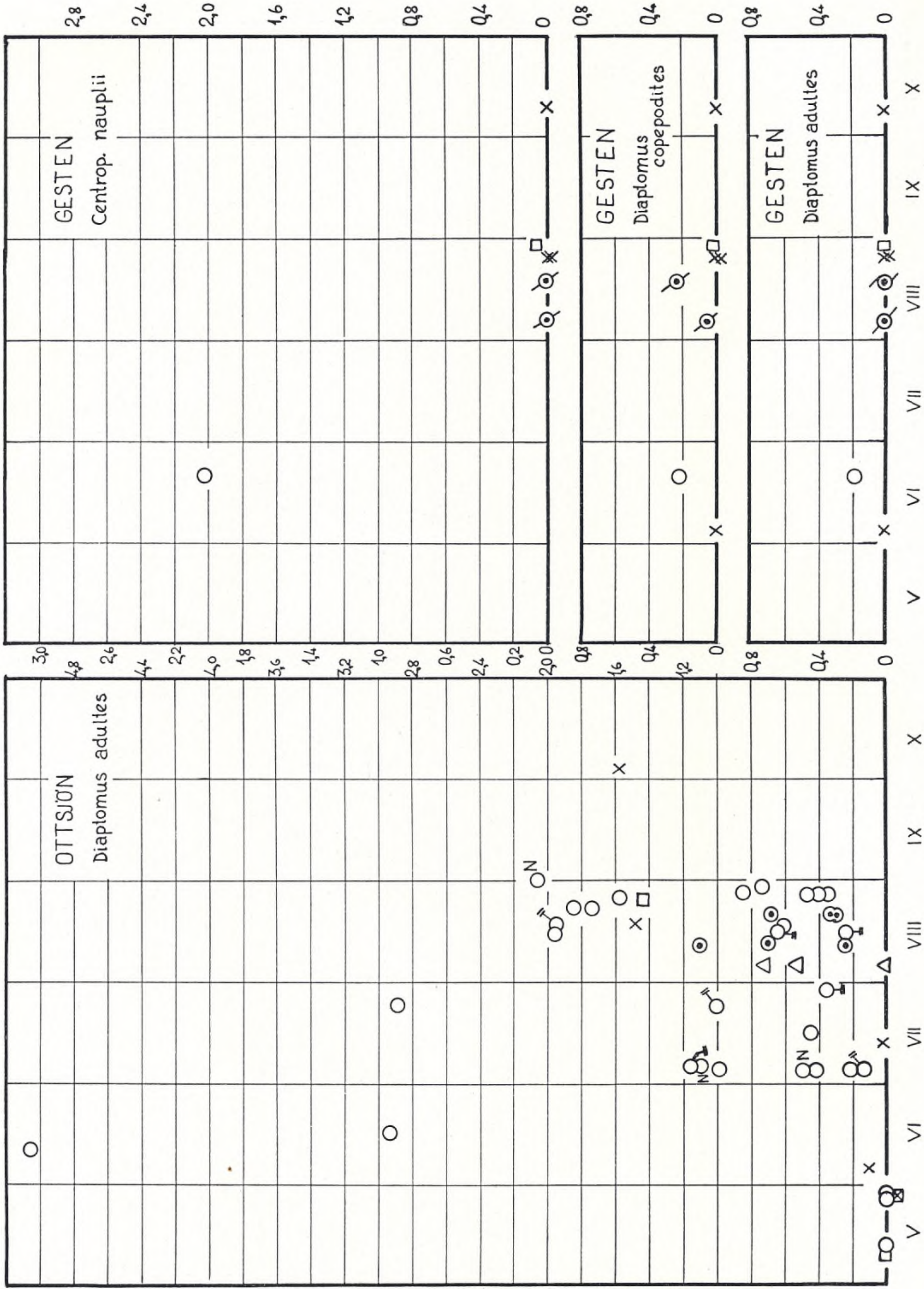
Lègende:

1946 ×	1950 ○	1957 △	Station auxiliaire	E	Ottsjön ♂
1947 ⊗	1951 ⊙	Avec épreuves de 2 m. ○̀ ⊙̀	» »	M, N, O	» ♀
1948 □	1955 ⊠	Sans » » 2 » Q Ⓠ	» »	D	Hottön ♂ □

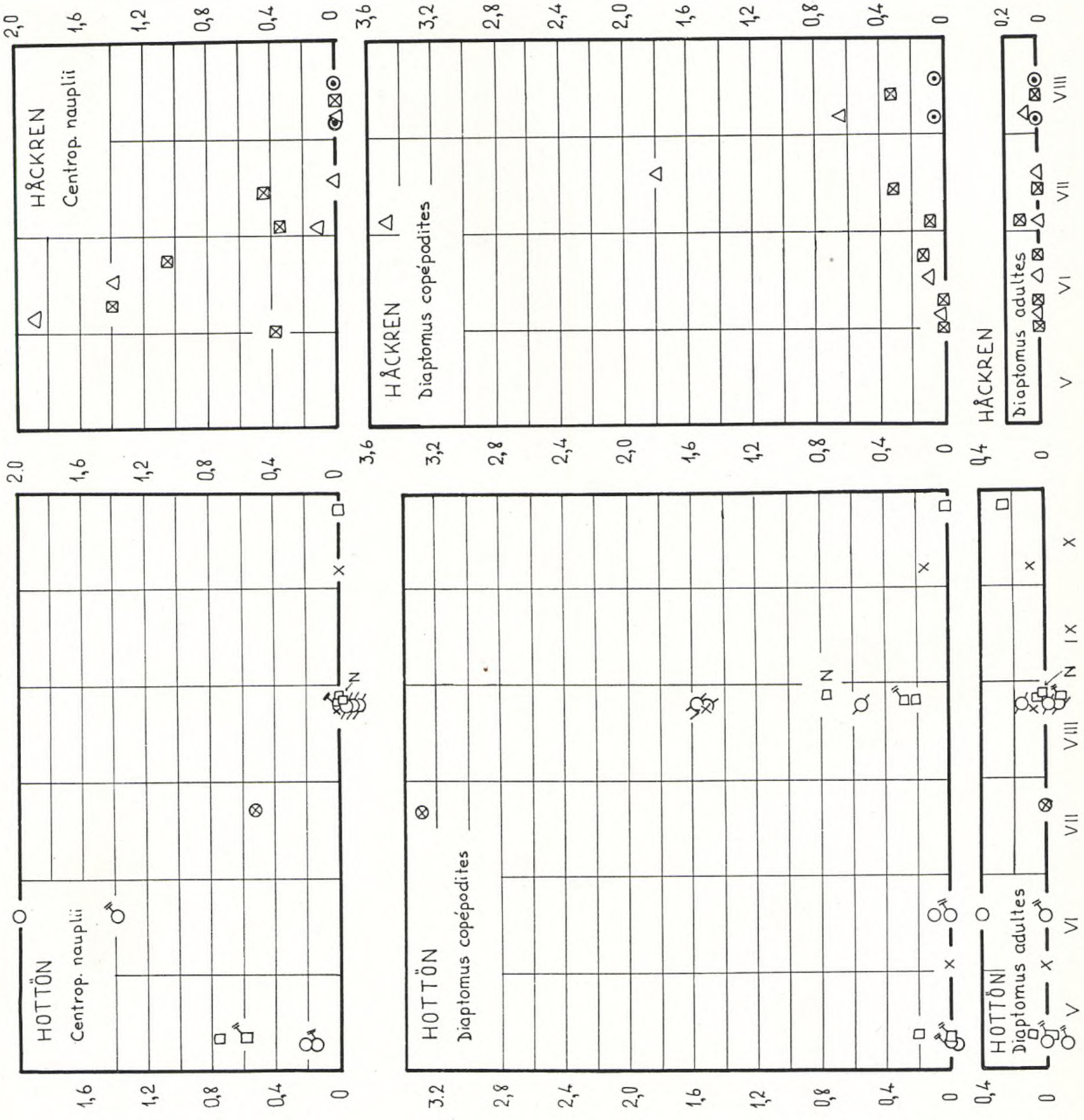

OTTSJÖ
Diaptomus copépodites
OTTSJÖ
Centrop. nauplii
4,0
3,6
3,2
2,8
2,4
2,0
1,6
1,2
0,8
0,4
0
V
VI
VII
VIII
IX
X
N

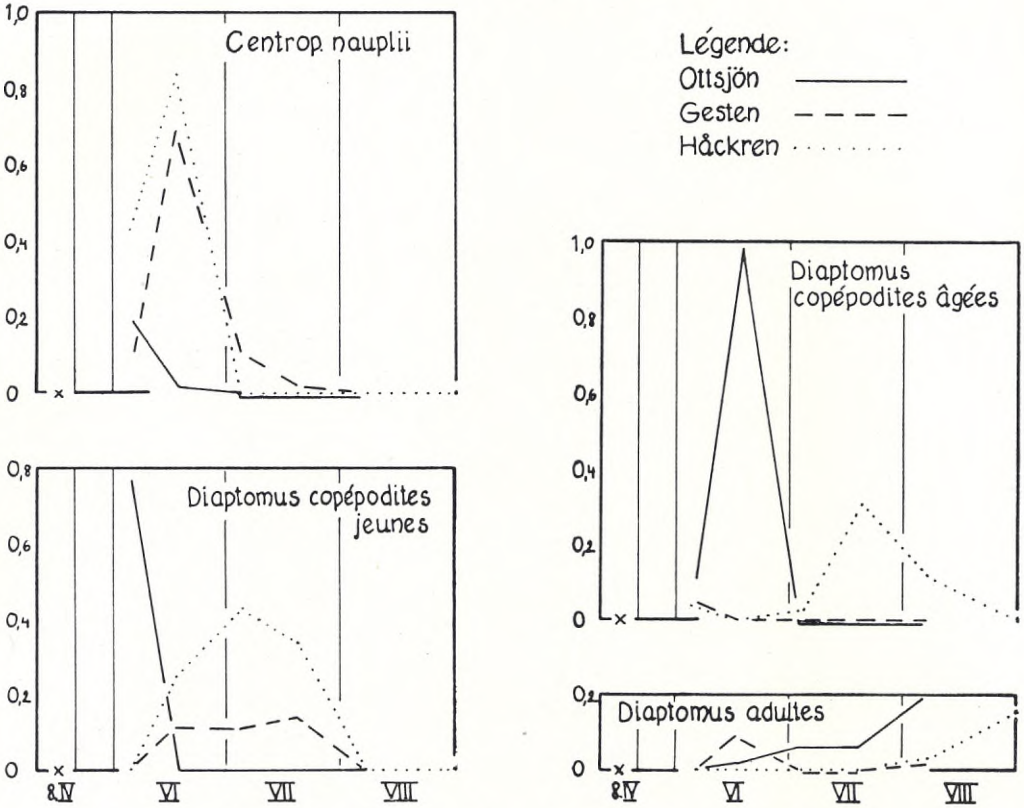
Graphique 2.

Graphique 3.


GESTEN
Centrop. nauplii
GESTEN
Diaptomus copepodites
GESTEN
Diaptomus adultes
OTTSJÖN
Diaptomus adultes
V
VI
VII
VIII
IX
X
0
0,4
0,8
1,2
1,6
2,0
2,4
2,8
3,2
3,6
4,0
4,4
4,8
0,2
0,6
1,0
1,4
1,8
2,2
2,6
3,0
N

Graphique 4.


HÅCKREN
Centrop. nauplii
2,0
1,6
1,2
0,8
0,4
0
HÅCKREN
Diaptomus copépodites
3,6
3,2
2,8
2,4
2,0
1,6
1,2
0,8
0,4
0
HÅCKREN
Diaptomus adultes
0.2
0
V
VI
VII
VIII
HOTTÖN
Centrop. nauplii
2.0
1,6
1,2
0,8
0,4
0
HOTTÖN
Diaptomus copépodites
3,6
3.2
2,8
2,4
2,0
1,6
1,2
0,8
0,4
0
HOTTÖN
Diaptomus adultes
0,4
0
N
V
VI
VII
VIII
IX
X

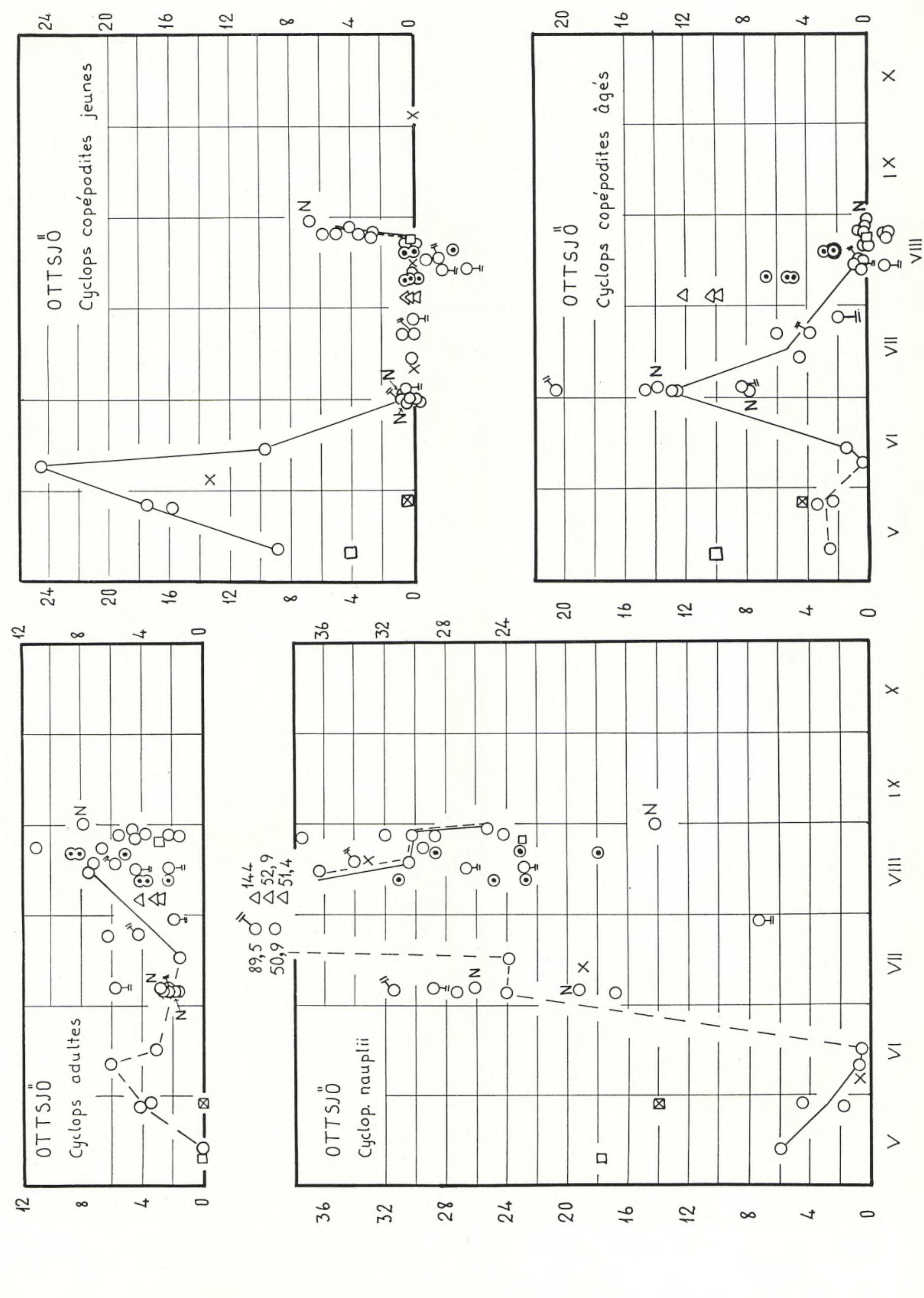


Graphique 5. *Diaptomus laticeps* dans des épreuves à la verticale, prises avec filet en 1957. Deux fractions dans Gesten. Rythme divergent du développement dans Ottsjön. Les graphiques 5 et 10 rendent compte de la densité moyenne par cinq litres, dans la colonne verticale, pourvu qu'une masse d'eau maximale ait traversé le filet. Les appréciations sont au dessous de la réalité. Copépodites I—III = jeunes, IV—V = âgés.

Graphiques 6—9. Densité moyenne par cinq litres dans la colonne verticale pour les *Cyclops scutifer*. Sars. Epreuves prises avec chercheur de planctons. Le courbe de la fraction A, dans Ottsjön en 1950 a été indiquée par une ligne, celle de la fraction B, par une suite de petits traits. Dans les autres lacs, les fractions n'ont pas été séparées, mais la fraction A existe avec certitude. Développement plus rapide de la fraction A dans Håckren que dans Ottsjön. En 1955 et 1957, lorsque l'analyse des différents stades a été plus approfondie, les copépodites IV et V ont été indiqués comme âgés. N = épreuves de nuit. Cf. aussi, explications des graphiques 2—4.

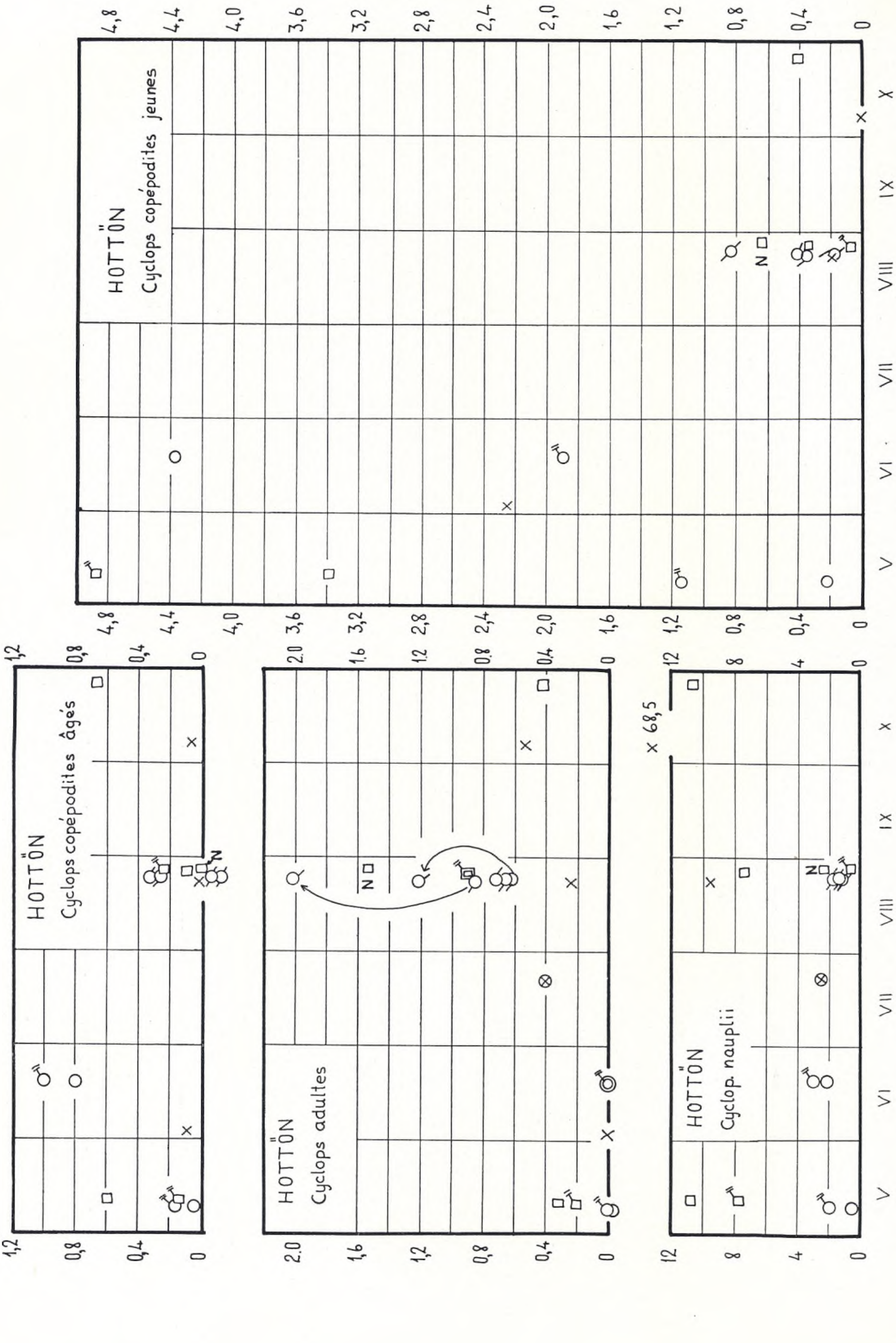
Lègende:

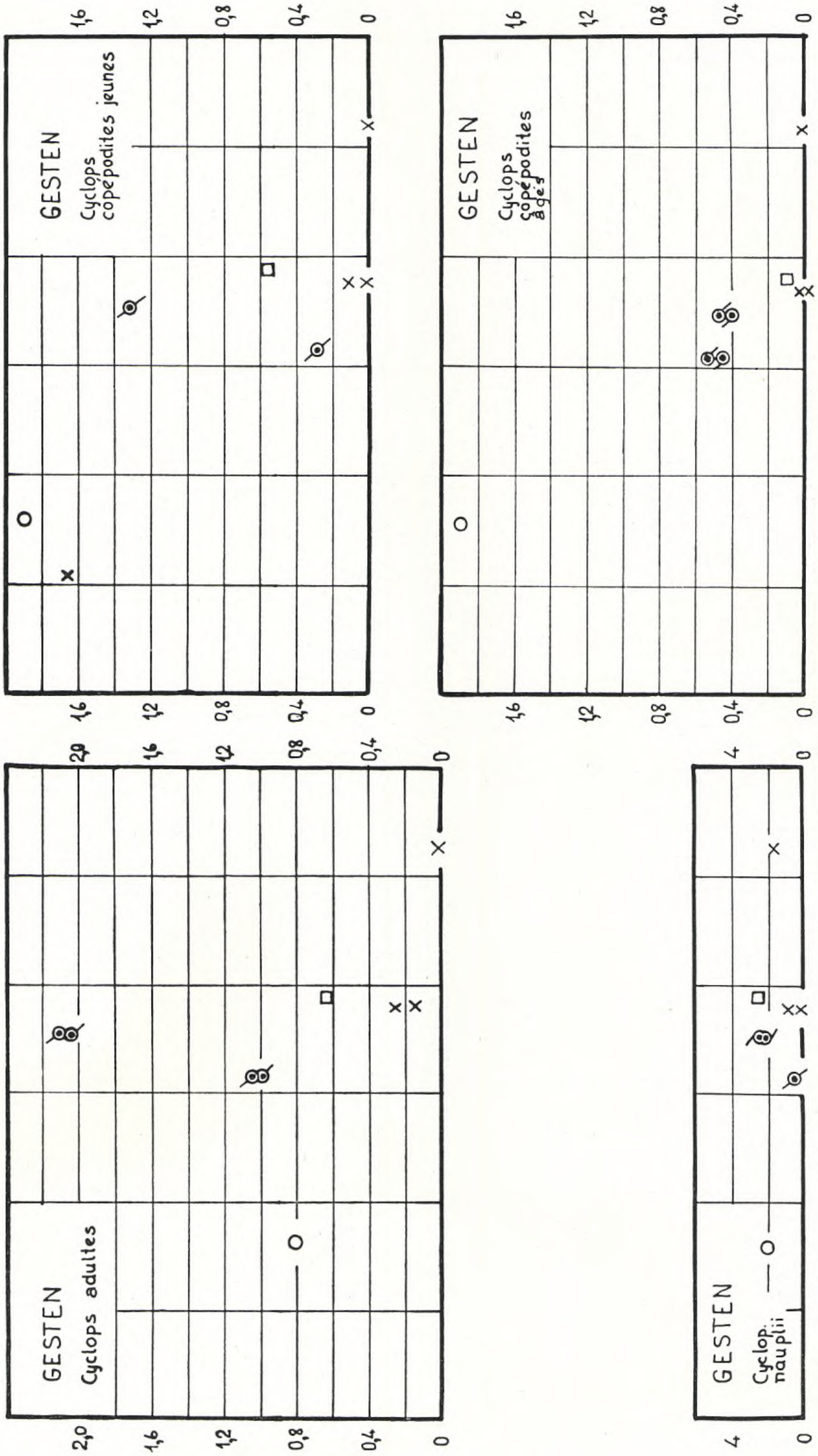
1946 × 1950 ○ **1957** △ **Station auxiliaire E Ottsjön** ♂
1947 ⊗ 1951 ⊙ » » **M, N, O** » ♀
1948 □ 1955 ☒ » » **D Hottön** ♂ □


OTTSJÖ
Cyclops copépodites jeunes
OTTSJÖ
Cyclops copépodites âgés
OTTSJÖ
Cyclops adultes
OTTSJÖ
Cyclop. nauplii
V
VI
VII
VIII
IX
X
N
X
0
4
8
12
16
20
24
28
32
36
89,5
50,9
144
52,9
51,4

Graphique 6.

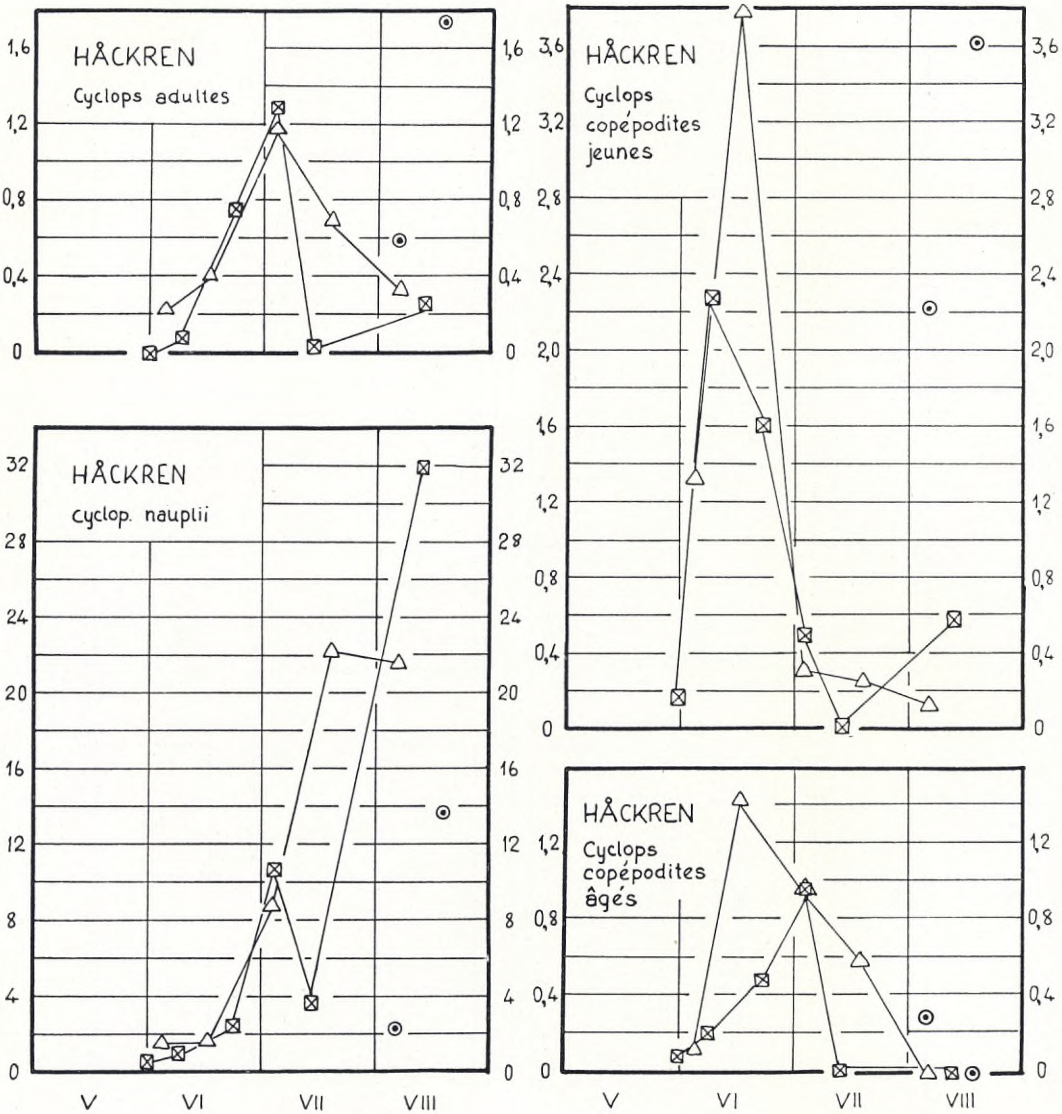
Graphique 7.


HOTTÖN
Cyclops copépodites jeunes
HOTTÖN
Cyclops copépodites âgés
HOTTÖN
Cyclops adultes
HOTTÖN
Cyclop. nauplii
V
VI
VII
VIII
IX
X
N
× 68,5
4,8
4,4
4,0
3,6
3,2
2,8
2,4
2,0
1,6
1,2
0,8
0,4
0
12
8
4


GESTEN
Cyclops copépodites jeunes
GESTEN
Cyclops copépodites âgés
GESTEN
Cyclops adultes
GESTEN
Cyclop. nauplii
0
0,4
0,8
1,2
1,6
2,0
4
V
VI
VII
VIII
IX
X

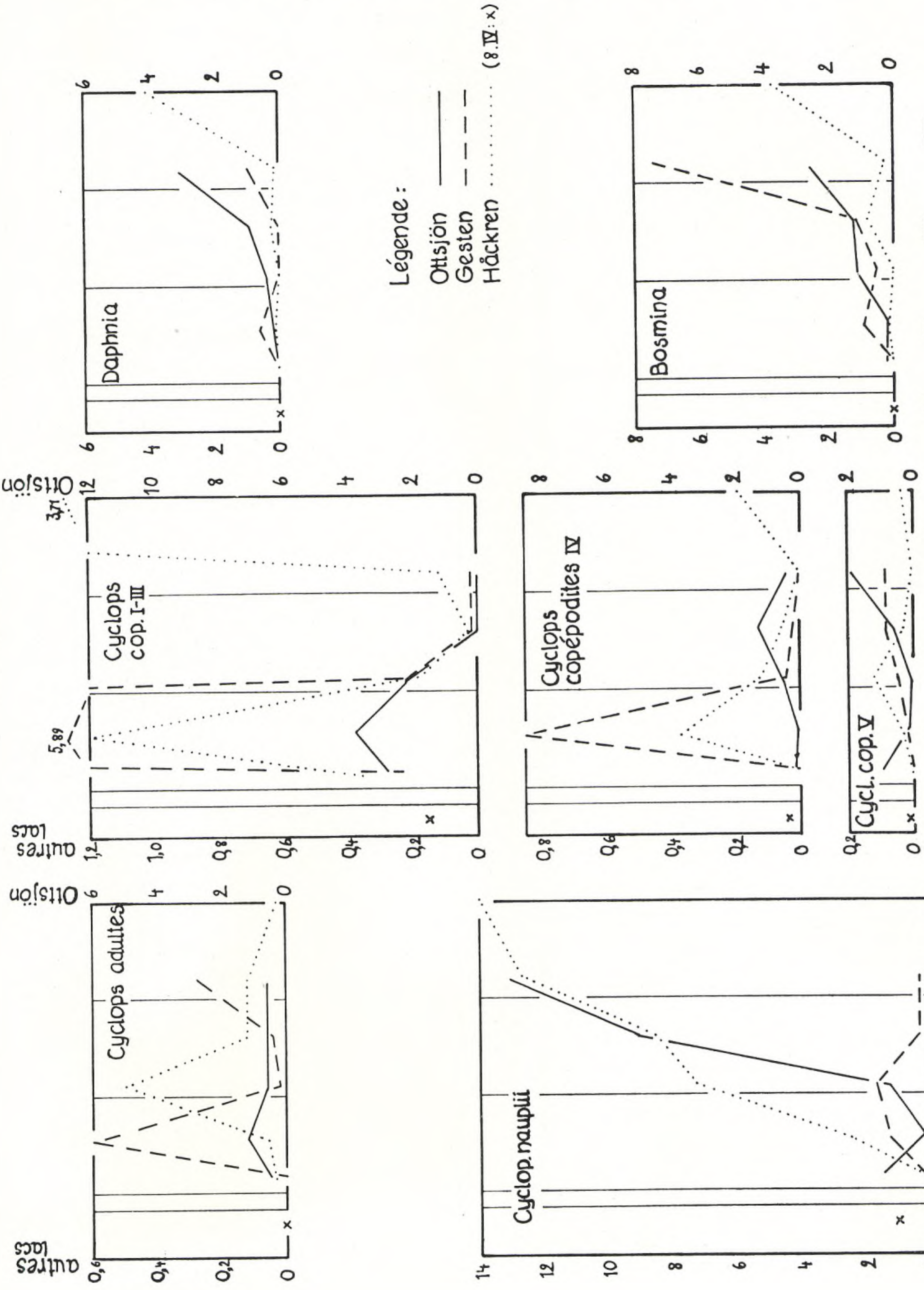
Graphique 8.

Graphique 9.



Graphique 10. *Cyclops scutifer, Daphnia longispina hyalina* et *Bosmina corégoni* dans épreuves à la verticale, prises avec filet, en 1957. Deux fractions *Cyclops* dans Ottsjön (pas soulignées spécialement), rythme de développement plus rapide pour la fraction A, dans Håckren que dans Ottsjön, mais développement plus rapide des populations Cladocères, dans Ottsjön que dans Håckren. Les diagrammes rendent compte de la densité moyenne de 5 litres, pourvu qu'une masse d'eau maximale ait traversé le filet.

Il est bon d'observer les deux échelles différentes.



Graphique 10.

Ånn, 31—3—46 (op. cit. p. 104) et de Håckren, 8—4—57. Durant l'hiver, cette pulsation doit s'arrêter, lorsque les copépodites deviennent âgés, la plupart nageant dans la région limnétique (Ottsjön) ou sont probablement couchés sur le fond (Håckren). Au moment de la débacle la pulsation devient par contre plus vigoureuse et donne naissance à la fraction A dans la population de *Cyclops*.

Le dualisme serait donc provoqué à nouveau chaque hiver. Le problème n'est pas pour autant résolu, mais seulement déplacé, il reste à découvrir la source de la production de nauplii.

Dans Gesten, les deux fractions semblent mieux séparées que dans Håckren. Hottön a été traité dans op. cit. p. 104, avec l'appui du matériel limité qui a été pris.

Sur un point la théorie du dualisme doit être modifiée. On peut penser que des nauplii des deux fractions peuvent contribuer à la pulsation des jeunes copépodites durant la fin de l'été dans tous les lacs. Il est donc possible que les adultes du printemps et du début de l'été aient produit plusieurs couvées de nauplii durant l'été qui ne se sont pas développées (proie des animaux prédateurs).

Indépendamment de la position adoptée à l'égard de l'existence des deux fractions dans Håckren, on peut conclure que dans ce lac, le développement des jeunes copépodites en *Cyclops* adultes, y est plus rapide que dans Ottsjön.

Les *Cyclops* sont concentrés dans la partie la plus profonde et la plus froide de Håckren durant tout l'été.

Il a été rendu-compte, en 1952, de certains traits du cycle annuel des Cladocères. On ne peut cloisonner de façon certaine, les différences entre les années et les differences entre les lacs (Tab. 7), mais les indices qui s'y révèlent suggèrent une différence entre les lacs. Les cycles annuels dans Ottsjön arrivent plus rapidement à leur point culminant que dans Hottön (1950) et Håckren (1951, *Daphnia,* 1957, *Bosmina* et *Daphnia,* Graph. 10, 11 et 12). Cependant en 1957, le maximum d'abondance était très retardé dans Ottsjön, ainsi qu'en 1951. Les épreuves de septembre font défaut. C'est pourquoi on ne peut exclure la possibilité d'un second maximum en septembre ou que le maximum d'août se maintient jusqu'en septembre. Certaines épreuves prises

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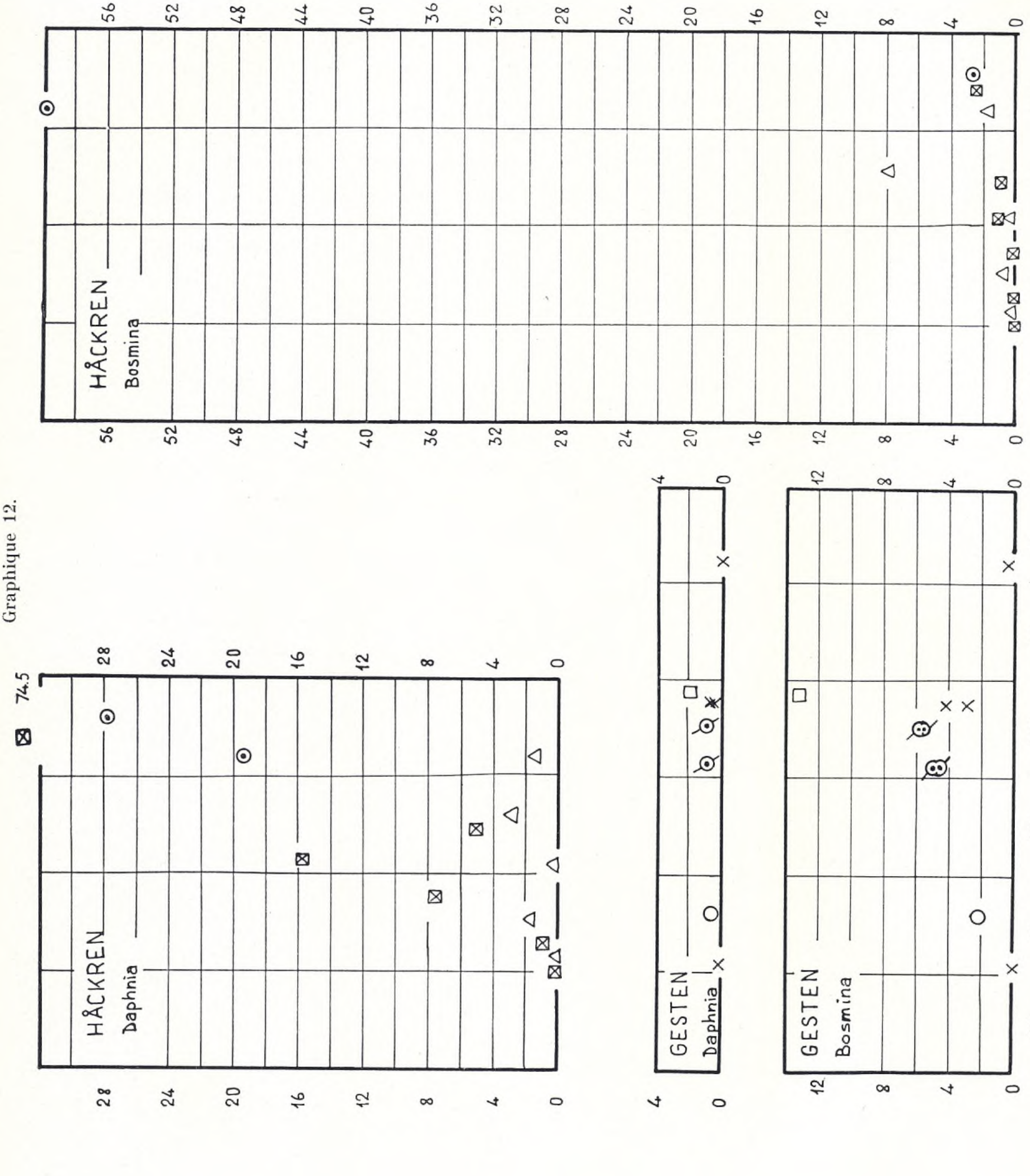
Graphiques 11—12. Densité moyenne par cinq litres dans la colonne verticale pour *Daphnia l. hyalina* LEYDIG et *Bosmina corégoni* BAIRD. Epreuves prises avec chercheur de planctons. Développement rapide des populations dans Ottsjön. N=épreuves de nuit. Cf. pour le reste, explications des graphiques 2—4.

Lègende:

1946 × 1950 ○ **1957** △ **Station auxiliaire E** **Ottsjön** ♂
1947 ⊗ 1951 ⊙ » » **M, N, O** » ♀
1948 □ 1955 ⊠ » » **D** **Hottön** ♂ □

Graphique 11.

Graphique 12.



à l'embouchure de Ånn, par MÜLLER (1956) font penser à cette possibilité à la condition qu'un chercheur de plancton et un filet muni d'hélice et de compteur donnent des résultats équivalents. La grandeur des densités qu'il a obtenues est un peu extraordinaire.

Pour illustrer davantage le cycle annuel, le tab. 4 établit les proportions de mâles et de femelles jeunes de toute la population de *Daphnia.*

La distribution verticale des différentes formes de *Daphnia* et de *Bosmina* durant le mois d'août 1955 suit le modèle présenté en 1952, basé sur du matériel pris au mois d'août. La distribution verticale dans Ottsjön 1957, s'écarte légèrement du modèle émis.

L'effet d'une débacle tardive sur la pulsation des populations au printemps

Dans le travail de 1952 il a été discuté de la différence entre les populations de plancton au cours des différentes années en tenant compte de la date de débacle.

En 1955 et en 1957 la débacle était tardive, d'ou la possibilité de vérifier les conclusions émises auparavant, ce qui était d'autant plus désirable que certaines dates de débacle dans op. cit. 1952, ne s'appuyaient pas sur une observation personnelle, mais avaient été fournies par des rapporteurs et leurs rapports différaient de ceux donnés par le personnel de l'Institut suédois de Météorologie et d'Hydrologie (Tab. 5).

Des indices certaines sur l'effet d'un déplacement de la débacle n'existent ni pour Ottsjön et Hottön 1948 ni pour Håckren 1955 et 1957. Ce n'est qu'en comparant le développement des populations de Ottsjön en 1950, 1953, 1955 et 1957, qu'il est possible de prendre parti (Graph. 2, 3, 5, 6, 10, 11 et Tab. 1). La population de *Diaptomus* passe du stade copépodite au stade adulte, la deuxième semaine de juin, lors des années à débacle précoce, 1950 et 1953, mais seulement après la mi-juin, lorsque la débacle est tardive, comme en 1957. Les points culminants en juin de jeunes copépodites et de *Cyclops* adultes, arrivent tardivement en 1957. Les *Bosmina* au milieu de juin, les *Daphnia* au début de juillet sont encore très peu nombreux en 1957. Finalement les indices ramassés de toutes espèces (*Cyclops, Diaptomus, Daphnia* et *Bosmina*) s'accordent lors d'un printemps extrèmement retardé, 1955, avec l'hypothèse, qu'une débacle tardive, retarde le cycle annuel des planctons crustacés. L'épreuve du 27—5 a été prise sous la glace. Les *Daphnia* étaient très peu nombreuses dans toutes les épreuves du mois de mai, en 1948, 1950 et 1955, mais parmi le petit nombre trouvé, toutes étaient jeunes en 1955, alors que quelques individus, en 1948 et en 1950, portaient des œufs dans leur chambre incubatrice. Les copépodites *Diaptomus* étaient principalement au stade I, le 27—5—1955, mais copépodites âgés le 26 et 27—5—1950. Les *Cyclops* adultes manquaient complètement en 1955.

En conclusion on peut dire que si la débacle est très retardée une année, on peut démontrer un retardement dans le cycle annuel des planctons crustacés.

Les populations pendant un été froid, après une débacle tardive

Les températures ont été prises à la verticale, dans les bassins les plus profonds des lacs, à l'aide d'un chercheur RUTTNER. Les thermomètres employés en 1950 et plus tard, ont été comparés avec un thermomètre étalon et les valeurs ont été corrigées. Celles de 1946 et 1948 ne l'ont pas été. Une comparaison avec la température de l'air à Östersund et à Storlien, donnée dans le rapport SMHI 1947—1958, rend pourtant possible une discussion des valeurs de 1946 et 1948, Graph. 13—14.

Si on constitue une moyenne des températures moyennes de l'air des mois de juillet et août, on voit qu'en 1951 et 1957, elles ont été sensiblement plus basses que celles des autres années. Ordinairement la température moyenne de l'air au mois de juillet est plus haute qu'en août. En 1950 et 1951 seulement, la situation était renversée. L'utilité des observations de température de l'eau en 1946 et 1948 (op. cit. 1952, Graph. 5 à 12) peut être appuyée par le fait que les températures observées en juillet 1946 sont plus élevées qu'en 1950, dans Ottsjön et par le fait que le métalimnion était posé plus bas dans Hottön, en 1948 qu'en 1950, ce qui est aussi l'expression d'un mois de juillet très chaud. (En 1946, ce dernier effet n'a pas lieu.) Au mois d'août 1946 et 1948, l'eau de surface qui réagit plus rapidement, est aussi plus froide qu'en 1950, dans Hottön.

Une différenciation entre les années 1946, 1948 et 1950, à la fin août, dans Ottsjön qui est remué et homotherme, n'est pas possible à établir avec les observations présentes sur la température de l'eau, mais les moyennes pour la température de l'air des trois mois d'été sont très près les unes des autres ces années là.

Ce qui suit, concernant les années 1950 à 1957, mérite d'être signalé:

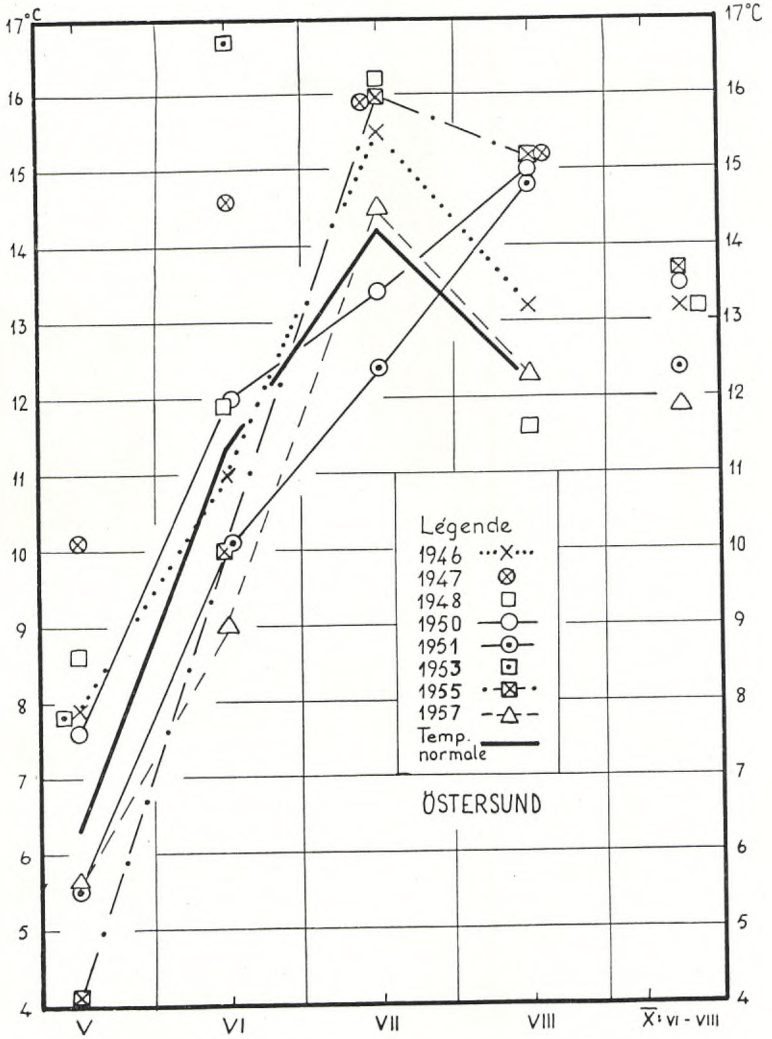
1) — Selon la température de l'eau pour les mois de juillet et août, 1950 était plus chaud et 1951 plus froid, et des deux années intermédiaires, 1955 est un peu plus chaud que 1957 (Graph. 15, 17). Si on s'en réfère à la température de l'air, on peut constater que la différence entre le mois d'août chaud de 1955 et le mois d'août froid de 1957, n'a pu avoir beaucoup d'effet au moment où les températures de l'eau ont été prises (et les épreuves de plancton prises).

2) — L'eau s'est réchauffée lentement en 1950, quoique la débacle ne fut pas tardive, mais à cause des grandes masses d'eau à réchauffer au moment de la grande crue de printemps survenue cette année là (Graph. 15, 18).

3) — L'eau s'est réchauffée irrégulièrement certaines années et très lentement à la fin de juin 1957 et fin juillet et début d'août 1955 et 1957.

4) — La débacle était tardive en 1951 et 1957, et extrémement tardive en 1955 (Tab. 5).

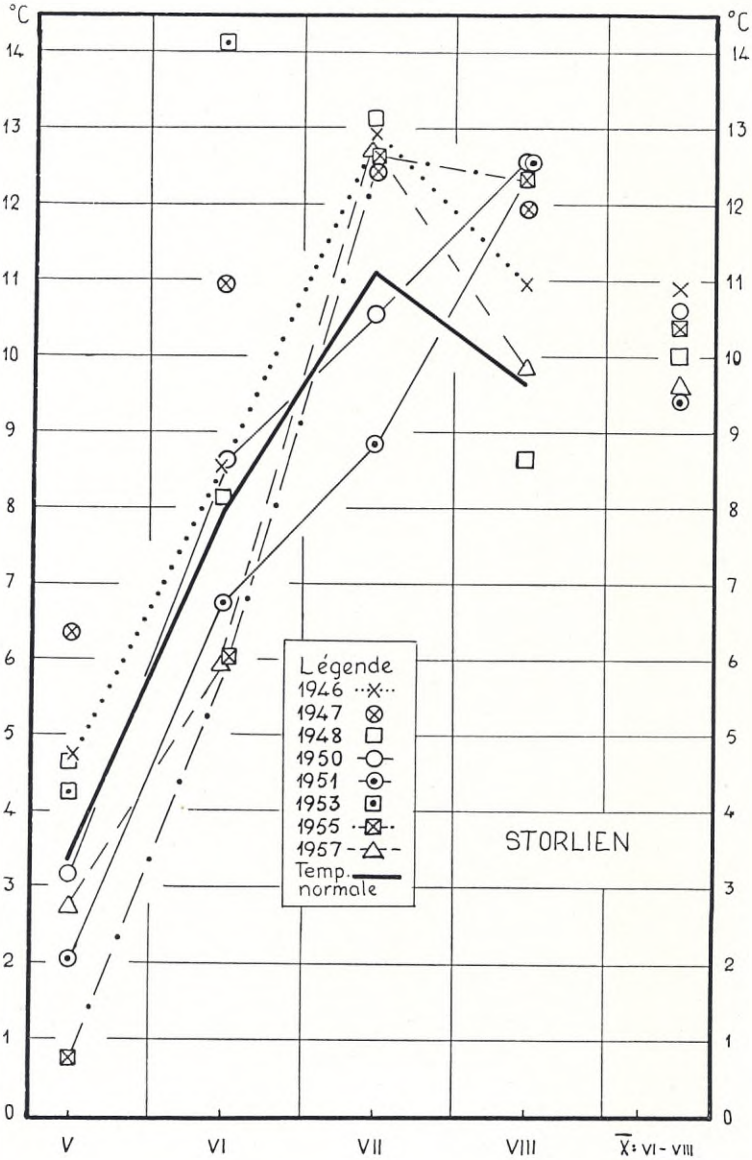
Graphique 13.



Graphiques 13—14. Température de l'air, Storlien et Östersund, moyennes par mois et moyenne pour la période juin-août ($X_{VI-VIII}$).

Le *Cyclops* a des maxima de densité qui passent rapidement et puisque la densité des individus à un certain stade de développement peut être une mauvaise mesure du nombre total si le stade est rapidement passé (Kofoid 1908, p. 280 — Marshall et alii 1934), les *Cyclops* ont été complètement retirés de la discussion des maxima de la densité. Les observations (Graph. 6, 9) peuvent être interprétées comme un retardement du cycle annuel de fraction A, pendant l'année 1951, qui était tardive et froide dans Ottsjön et Håck-

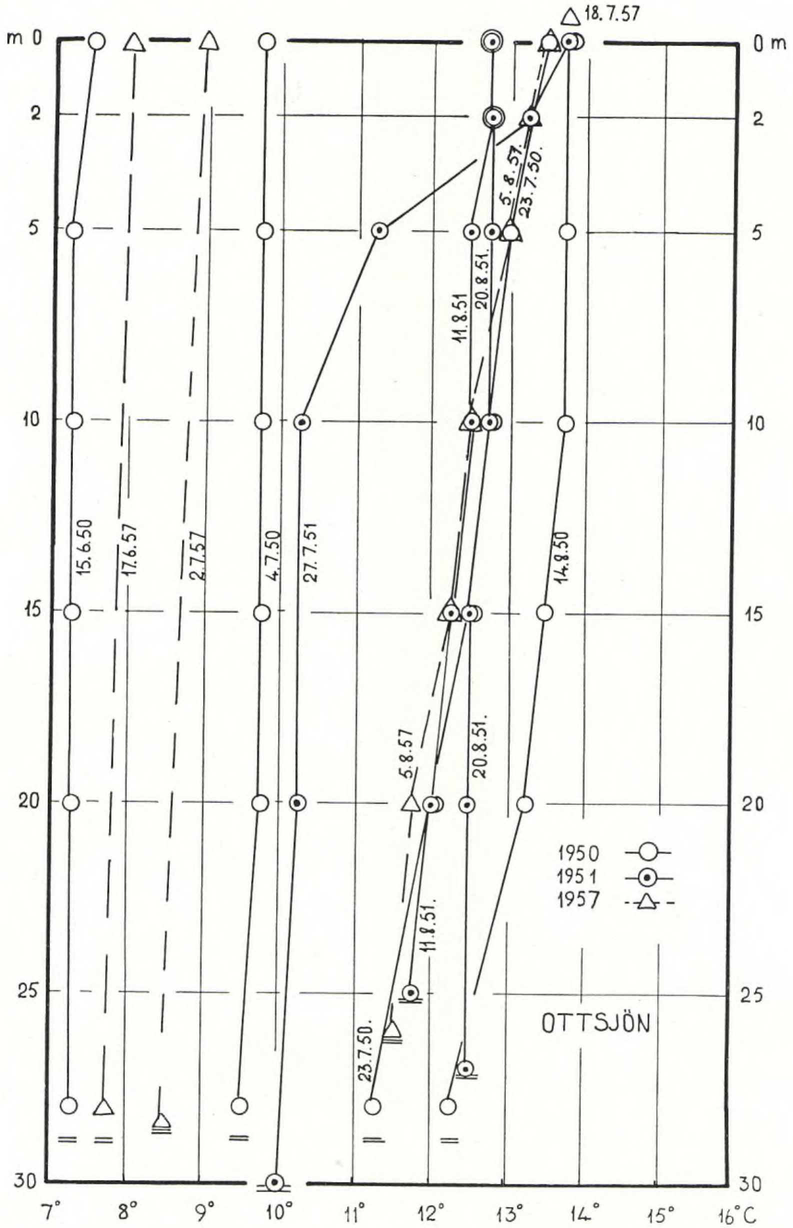
Graphique 14.



ren où la transformation de copépodites âgés en adultes se passe rarement tard, en août. Ceci est valable aussi pour Ottsjön en 1957.

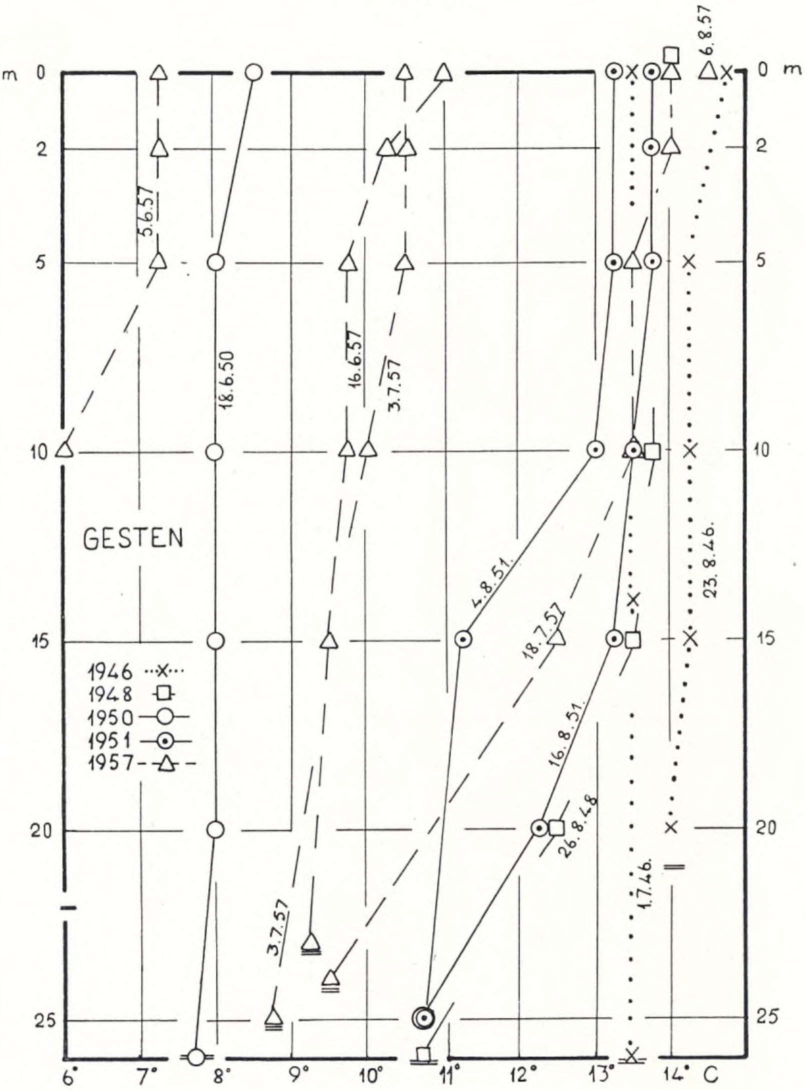
En août les nauplii se transforment en jeunes copépodites; le fait arrive tôt dans Håckren et Gesten l'année froide 1951, mais tard, dans Ottsjön en 1948, année où la débacle arrive de bonne heure. On ne peut parler d'un aspect automnal précoce en 1951, car la température de l'air, au mois d'août,

Graphique 15.



Graphiques 15—17. Température de l'eau, Ottsjön, Gesten et Håckren. Autres indications dans le travail de 1952. Ce signe (=) mis au dessous de celui de la température la plus basse, indique le fond du lac. A partir de 1950, les valeurs sont corrigées.

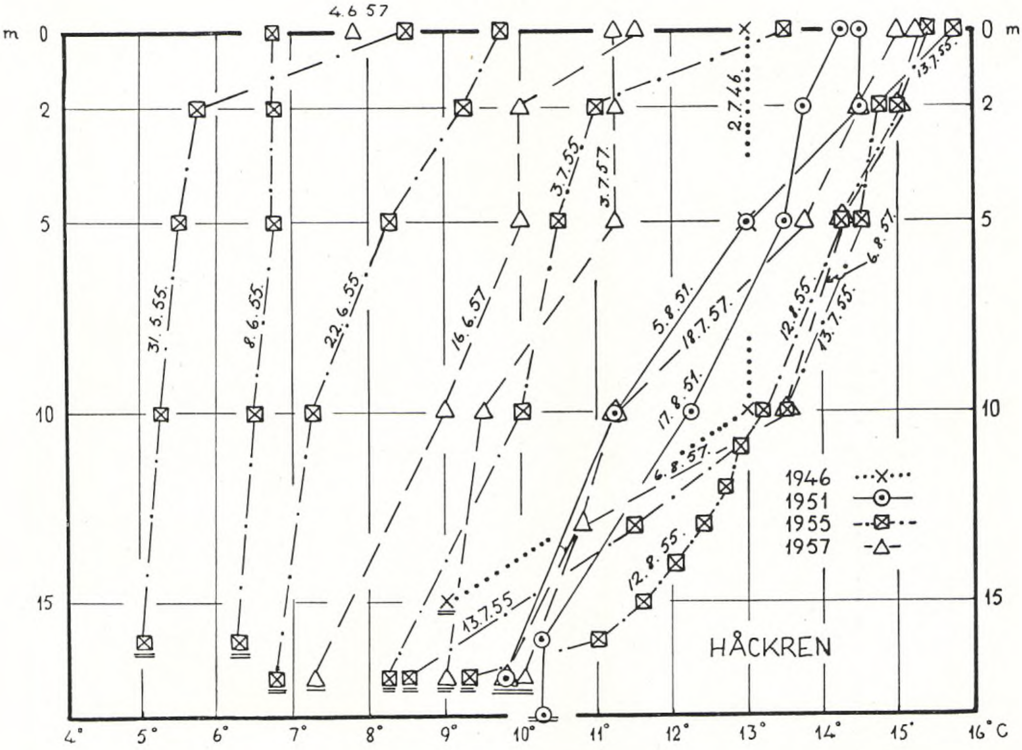
Graphique 16.



correspondait à une température d'un juillet normal. Il n'est pas possible de dire, pour le moment, le rôle joué par la température dans le complexe de facteurs qui régit la pulsation de fin d'été des copépodites jeunes.

Les valeurs basses de densité de *Diaptomus* adultes en 1951 et 1957, et les valeurs de densités élevées de *Daphnia* en 1957 et *Bosmina* en 1951 et 1957, toutes de Ottsjön, au mois d'août, reflètent des retardements dans le cycle annuel. Comme la courbe de *Diaptomus* adultes en 1957 (Graph. 5) monte de juillet à août, cela laisse à penser que la pauvreté de *Diaptomus* de juillet est

Graphique 17.



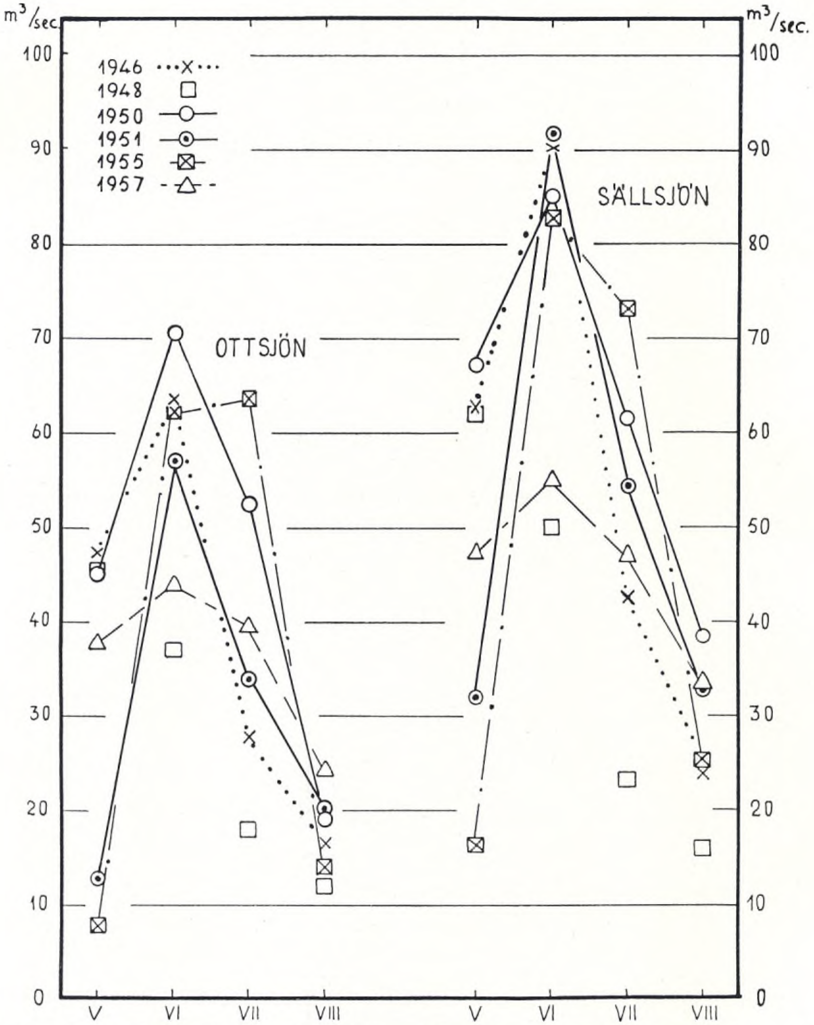
spécialement prononcée les années froides. La moyenne de densité des *Bosmina* en 1951 et 1957 est plus élevée dans les épreuves d'août qu'au moment du point culminant de la courbe de juin-juillet 1950. La différence n'est pas significative (Tab. 6).

Dans Håckren, les bonds entre les valeurs de densités élevées et basses, en août, sont tellement forts qu'on ne peut rien bâtir sur ces observations. Dans Gesten, les valeurs de densité, de l'année 1951, pour *Bosmina* et *Daphnia,* sont situées entre celles de 1948 et celles de 1946. S'il faut en tirer une conclusion, il faut plutôt parler du débit exceptionnellement bas en 1948 comme explication pour les valeurs plus élevées de cette année là (cf. l'introduction).

Les stations auxiliaires — Stabilité des populations de plancton

Des dénominations particulières ont été données, dans les Graph. 2—4, 6, 7, 11 aux abondances provenant des stations auxiliaires D, dans Hottön (1948 et 1950) et M, N, O, et E, dans Ottsjön (1950).

La température à la station E, dans Ottsjön, était de 1/4 à 1/2 degrés plus



Graphique 18. Débit à l'émissaire de Ottsjön et de Sällsjön (lac le plus proche en dessous de Håckren), selon l'Institut suédois de Météorologie et d'Hydrologie.

bas qu'à la station centrale A, dans la partie inférieure de la verticale, le 4—7 et 23—7, mais presque identique à la température de la station centrale le 17—8. Les valeurs moins élevées de E, en juillet, peuvent s'expliquer du fait que l'eau froide pénètre dans le lac par l'affluent sud, cf. le travail 1952, carte 3. (Les indications 6°, 7°, et 8°, manquent dans le graphique de op. cit. 7, où les températures rendent compte des stations S et U.) La température des stations M—N—O est généralement un peu plus basse qu'à la station centrale, cf. op. cit. p. 123. Dans un certain sens, il y a une ressemblance entre les stations M—N—O dans Ottsjön 1950, et la station centrale lors d'une année froide: La densité de *Diaptomus* adultes est très basse au mois d'août.

Il est bon de remarquer que la densité de *Bosmina* descend rapidement dans E, mais pour le reste, la concordance entre les stations auxiliaires et la station centrale est frappante. Cette ressemblance est surtout une ressemblance du rythme annuel et ne doit pas être présentée comme un argument contre une répartition hétérogène horizontale. Une telle répartition a été signalée dans l'eau douce par BALDI et alii en 1945, 1947, et dans un grand nombre de travaux du milieu marin (cf. aussi LINDSTRÖM 1952, p. 92—94, 112).

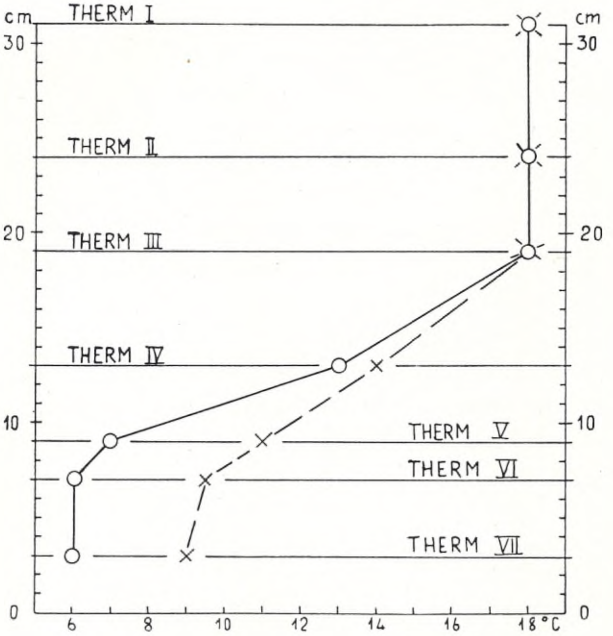
Cependant il doit être difficile d'évaluer une irrégularité trouvée dans la répartition horizontale. D'une part, il y a une forte formation d'essaims dans la répartition détaillée des planctons qui probablement est plus accentuée dans les endroits abrités (discussion, TONOLLI 1949, LINDSTRÖM 1957). D'autre part, on doit compter avec de rapides fluctuations, dans certaines populations (SLOBODKIN 1954), qui n'ont pas besoin d'être conformes dans toutes les parties d'un lac, à cela s'ajoute des différences plus profondes entre les stations. Il est évidemment aléatoire d'avancer d'un pas et de discuter le degrés de stabilité dans les lacs. Les chapitres qui précèdent et les graphiques sont les apports que je puis apporter à cette discussion.

L'influence de la température et de la lumière sur les mouvements des Daphnia

L'expérimentation qui suit n'avait qu'un seul but, vérifier si les résultats des auteurs antérieurs pouvaient s'appliquer aux populations de *Daphnia* qui existent dans les lacs du Jämtland.

Des *Daphnia longispina hyalina* de Ånn, fraîchement pêchées à la surface de Ånn, ont été gardées dans une eau à une température de 19°C et à la lumière du jour (voir plus loin), à côté de la cuvette à expérience. Cette cuvette de forme parallélépipédique droite, en plastique, était placée sur un champ à l'ombre d'un grand bâtiment. La lumière qui la traversait a été mesurée à l'aide d'un photométre Weston Master II (B 0324), elle variait entre 100° et 400° au cours des expérimentations 1 et 3. Ceci se passait le 19.8.55 entre 14h 40 et 15h 35. La température était mesurée avec des thermométres dont les uns traversaient les parois de la cuvette, d'autres étaient accrochés à l'intérieur. L'eau provenait de Ånn et avait été prise à un robinet et non filtrée. Les *Daphnia* ont été transvasées dans la cuvette à l'aide d'une pipette. Durant les premières secondes de toutes les expérimentations les animaux restèrent passifs.

Expérimentation 1. — Les stratifications de la température ressortent du graph. 19. Deux individus se tenaient dans une position droite jusqu'à ce qu'ils eurent atteint le fond, l'un après 80 secondes, l'autre après 205 secondes. Un troisième nageait la tête en bas et atteignit le fond après 37 secondes.



Graphique 19. Température dans la cuvette à expérimentation. o——o 14h 38 et ×——× 15h 20. Echelle perpendiculaire donnant la profondeur à partir du fond. Le thermomètre I, a été placé à la surface.

Cette nage active vers le bas a été signalée par EWALD (1910), ESTERLY (1911, 1919), SIEDENTOP (1930), WORTHINGTON (1931), CLARKE (1934 c), FOXON (1934), HARDY et BAINBRIDGE (1954) et observée dans la nature par BAINBRIDGE (1952). Les 16 autres exemplaires d'animaux d'expérimentation, après les premières secondes de passivité, se mirent en route en nageant vivement la tête en bas. Des seize animaux, onze se sont retournés pour nager dans la position droite entre le thermomètre nr 3 et le nr 5, ou au thermomètre nr 5, après 21 secondes, en moyenne, et malgré leur position droite, ont sombré vers le fond qu'ils atteignaient, en moyenne, 54 secondes après avoir été placés dans la cuvette. Les cinq animaux restants ne se sont retournés qu'au thermomètre nr 6, après, en moyenne, 24 secondes et atteignirent le fond après 45 secondes, en moyenne.

Les 16 animaux, dont il vient d'être question, descendaient plus lentement vers la fin du parcours, sauf un qui gardait sa vitesse.

Expérimentation 2. — Température comme dans l'expérimentation précédente. La cuvette était couverte, sur trois côtés, de papier foncé. Des 10 animaux employés, aucun ne nageait la tête en bas, mais ils atteignaient le fond dans une position droite.

Expérimentation 3. — Les conditions de lumière comme dans l'expérimentation 1. Température dans toute la cuvette, 15° centigrades. Deux individus gardèrent longtemps la position droite. Un troisième avait la tête dirigée tantôt vers le haut, tantôt vers le bas, mais retrouva pour finir la surface.

Les 17 autres animaux parvinrent au fond. 13, activement nageant, gardèrent sans interruption la tête dirigée vers le bas. 4 gardèrent la tête tantôt vers le haut, tantôt vers le bas. Pourtant à partir du dernier termomètre ils gardèrent la tête vers le bas.

D'autres auteurs ont démontré que les réactions des planctons crustacés, provoquées par le facteur lumière, sont modifiées par la température (références suivent). Il y a donc lieu de croire que les *Daphnia* dans Ånn réagissent d'une manière semblable, même si on peut critiquer l'installation assez primitive de mes expérimentations.

L'importance de la température et la compétition dans la complexité du milieu naturel

Dans leurs expérimentations de laboratoire, ROSE (1925), BROWN (1929), SIEDENTOP (1930) et ELSTER (1936), ont étudié les mouvements des planctons crustacés à des températures différentes et leurs réactions au contact de l'eau plus chaude ou plus froide. ROSE a aussi fait des expérimentations de choix; les animaux ont pu choisir entre des eaux à des températures différentes, sous des conditions de lumière constante. BIRGE (1897), LOEB (1908), STEUER (1901, 1910, avec références), RUSSEL (1927 a avec références), SIEDENTOP (1930) et CLARKE (1932) ont discuté ou démontré dans des expérimentations de laboratoire, que les mouvements des animaux, conditionnés par la lumière, sont modifiés par les changements de température. Cf., cependant, RUSSEL (1927) et CUSHING (1955 p. 151).

BROOKS et HUTCHINSON (1950) ont montré que la vitesse de descente est influencée par la viscosité de l'eau. Autant que je sache, il n'a pas été fait d'expérimentations où l'effet du facteur température et du facteur viscosité sur les mouvements propres des planctons aient été séparés dans un milieu sans nourriture. Mais l'exposé de LOEB (1908), sur les mouvements des animaux pour éviter la lumière, arrêtés par une baisse de température, fournit peut-être l'explication la plus probable aux rassemblements dans le métalimnion décrits par RUTTNER (1914), et par d'autres — cela ne comporte pas une actualisation des autres aspects de la théorie de LOEB. Les animaux réagiraient donc à une différence de température tandis qu'un changement de viscosité dans le métalimnion peut donc être présumé comme un des facteurs éloignés rentrant dans le complexe des facteurs qui ont donné à la réaction mentionnée au sujet de la température, une valeur positive pour la sélection naturelle (cf. LINDSTRÖM 1952 p. 107—109).

L'effet du facteur lumière, sur les migrations verticales des planctons crustacés, est cependant tellement dominant, que BURCKHARDT (1900), ESTERLY (1912), WOLTERECK (1930), WORTHINGTON (1931), CLARKE (1934), ELSTER (1936), et RUTTNER (1938) ont eu des motifs pour souligner la tolérance des planctons crustacés à des changements de température, puisque ceux-ci se meuvent sous de grands écarts de température pendant leur migration diurne dirigée par la lumière.

La température et la provision de nourriture agissent sur la vitesse de développement, ce qui a été démontré par des expérimentations de laboratoire. Les températures de léthalité ont été notées et l'importance du facteur température sur le recrutement et la mortalité et sur l'ampleur des couvées ont aussi été étudiées en laboratoire. On peut trouver des références sur ces différents points dans la bibliographie, aux signes (*).

Dans le milieu naturel, l'effet du facteur température sur le recrutement et la mortalité doit pouvoir être modifié par beaucoup d'autres facteurs et le facteur température peut aussi agir sur les populations par des canaux indirects (abondance de nourriture, prédateurs, parasites . . .).

La répartition verticale, la vitesse de développement, le recrutement et la mortalité dépendent de la température et cette dépendance doit être influencée par des formes planctoniques compétitrices. Des crustacés filtrants, comme les *Daphnia,* les *Bosmina* et les *Diaptomus* peuvent être supposés en compétition pour la nourriture, même si la sélectivité de l'appareil filtrant des planctons crustacés est plus sensible, qu'on ne l'a cru auparavant. Nous ignorons l'échelle de cette compétition (résumés d'articles de YOUNG 1928 et JØRGENSEN 1955; cf. aussi ERIKSSON 1934, COKER et HAYES 1940, EDMONDSON 1957). Le résultat de FRYER (1954) — deux espèces de *Diaptomus* dans un lac qui mangeaient de la nourriture différente — est un argument de poids contre des hypothèses trop hativement construites au sujet de la compétition entre les filtrateurs.

Le facteur compétition a déjà été discuté par BIRGE (1897 p. 365), STEUER (1901) et ESTERLY (1912), plus tard par ELTON (1929) et LOWNDES (1929), mais son importance pour le choix de l'habitat a été contesté. KOFOID (1907) a posé le problème de savoir si des espèces proches parentes pouvaient avoir une distribution coïncidente ou contiguë. Plus tard on a trouvé des cas où deux espèces de *Bosmina,* deux espèces Cyclopoïdes ou deux et même trois espèces de *Daphnia* habitaient des couches verticales différentes ou des régions différentes dans un lac. (FREIDENFELT 1913, WOLTERECK 1932, avec références, AURICH 1933, KIEFER 1940, RUTTNER 1952, PENNAK 1957 avec références et un résumé de la littérature *Bosmina* dans mon travail personnel de 1957).

On peut résumer comme suit l'état actuel des recherches: Les limites entre les habitats des différentes espèces sont souvent moins claires que dans les exemples qui viennent d'être cités. Quoique la nourriture pour les espèces compétitrices est probablement commune de temps en temps, et quoique les époques de l'année pendant lesquelles elles peuvent apparaître puissent coïncider dans une large mesure, malgré cela un certain isolement s'est formé qui leur permet de coexister dans le même lac. (cf. HUTCHINSON 1951, RILEY

1953, Bossone et Tonolli 1954, Ravera 1954, Smyly 1955, Pennak 1957, Lindström 1957).

Dans des expérimentations d'aquarium, Pacaud (1949) et Frank (1952, 1957) ont démontré l'effet vigoureux de la compétition dans un milieu uniforme.

Il n'est pas dans mon intention de résumer la grande littérature sur la répartition géographique, la répartition en profondeur et le mode d'apparition pendant l'année (cf. Brown 1929). On peut par une étude des trois thèmes mentionnés en venir à certaines caractéristiques de température pour des formes différentes (Ruttner 1938, Findenegg 1943) mais elles ne peuvent être valables sans réserves importantes qui ont été exposées par Ruttner à la page 293 dans op. cit. La découverte par Banta et Wood (1928) et Johnson (1952) de races thermales, et le travail de Worthington (1931) apportent encore des arguments contre une application trop généralisée des caractéristiques de la température qui ont été trouvées valables dans une région limitée.

Ce qui a été dit jusqu'ici, n'incline pas à penser que la température ait une influence, si bien connue, sur la densité des populations de plancton, dans la complexité du milieu naturel, qu'on puisse prédire comment une année froide ou chaude va influencer la composition et la quantité totale des planctons crustacés. Mais c'est une hypothèse de travail raisonnable que d'admettre qu'il puisse y avoir de tels changements.

Des observations à l'appui de cette hypothèse ont été faites par Marsh (1903) et Rawson (1956), pour ne signaler qu'un travail ancien et un travail récent sur ce thème. Bien d'autres auteurs depuis Birge (1897), Zschokke (1900) et Burckhardt (1900), ont trouvé un lien entre le cycle annuel de la température et le cycle annuel des planctons crustacés et aussi le fait qu'une pulsation forte dans la densité de la population suit le réchauffement de printemps.

Le résumé précédent va nous servir pour discuter les observations personnelles faites dans les lacs du Jämtland.

L'hiver, avec son manque de lumière et ses températures rigoureuses dans les lacs septentrionaux et alpins, a été décrit comme une période à production basse de phytoplancton, d'où découle une période pauvre en plancton crustacé. Cette généralisation n'épuise pas toutes les possibilités. Il faut compter avec une certaine endurance à la disette chez les planctons crustacés (Kerb 1910, Coker 1933, Fuller et Clarke 1936, Clarke 1939).

Une abondance de zooplancton au mois d'avril, dans Torne träsk, un des lacs septentrionaux de la Suède, a été signalée par Ekman et alii (1950) et Rodhe (1955), ainsi que l'existence de nourriture à la même époque. On peut se demander jusqu'à quel point il est utile de réviser la généralisation faite auparavant. Cela dépend de la composition des planctons crustacés, de filtrateurs ou d'animaux qui agrippent leur nourriture.

Dans du matériel ramassé auparavant dans Jämtland, il a été principalement trouvé des *Cyclops* nauplii et des copépodites âgés pendant l'hiver. Cela a été interprèté comme l'expression d'un manque général de nourriture (1952). Le matériel pris depuis, en hiver, a quelque peu modifié mes opinions (voir précédemment page 104). Mais pour comprendre l'aspect d'hiver il est tout de même essentiel de ne pas oublier que la capacité du groupe *Cyclops* à survivre aux périodes ingrates est essentiellement lié au stade copépodites âgés si les animaux se sont revêtus d'une carapace, ou reposent sur le fond, ou sont seulement arretés dans leur développement par un manque de nourriture (FRYER et SMYLY 1954, avec références. Voir aussi NORDQUIST 1921, COKER 1933, ELGMORK 1955 et COLE 1955).

Des données de travaux marins indiquent que les stades copépodites âgés remplissent les mêmes fonctions chez certains Calanoides (NICHOLLS 1933, MARSHALL et alii 1934, FISH 1936, CLARKE et ZINN 1937, USSING 1938, CLARKE 1939, JESPERSEN 1939, FILTEAU et TREMBLAY 1953, MARSHALL et ORR 1955). Une fraction de *Diaptomus* a été trouvée en hiver dans quelques uns des lacs du Jämtland avec des copépodites et au printemps avec des adultes.

D'ailleurs les filtrateurs passent l'hiver comme oeufs durables.

Un retardement des cycles annuels des planctons crustacés au cours des années à débacle tardive a été démontré aussi dans cette étude. La débacle, facile à observer à cause de sa marche dramatique n'est pas tout à fait un phénomène simple. La lumière qui transperce la glace augmente avant que la débacle n'ait lieu (EKMAN et alii 1950; la neige fond généralement avant la débacle), en concomitance la provision de nourriture peut augmenter. L'augmentation de nourriture, quelque soit l'époque où elle se produit, peut causer une pulsation dans la fraction B des *Cyclops* et des *Diaptomus,* dans des lacs où des copépodites âgés passent l'hiver dans l'eau sans entrer en engourdissement. (L'autre fraction *Cyclops* peut aussi subir cette influence.) Les copépodites âgés peuvent atteindre rapidement la maturité sexuelle. Le risque d'apparition de couvées manquées semble ici bien petit puisque l'impulsion donnée au développement est en augmentation avec la provision de nourriture. Quelque soit la cause du réveil des œufs durables hibernants, (VOLLMER 1912, WOOD et BANTA 1937, COMITA 1956), le dernier facteur qui régit n'est guère une augmentation de la provision de nourriture. Si le potentiel de recrutement dépend de l'existence d'œufs durables, hibernants, le risque de parution de couvées manquées semble plus grand puisqu'il n'y a pas de certitude d'existence de nourriture convenable au temps voulu, chaque année. Cependant, au sujet des *Heterocope,* ELSTER (1955) a signalé un mécanisme de sureté. Celui-ci consiste dans le fait que l'éclosion s'étend sur un grand espace de temps. La mortalité est élevée dans la plupart des cas. BIRGE a décrit un cas parallèle (1897) où une température élevée à fait sortir une population de *Cyclops,* d'une importance trop grande pour son milieu, par une éclosion d'œufs activée.

La limite entre différentes familles de Copépodes ne coïncide pas avec les façons différentes de démarrer une pulsation de printemps.

Le cycle annuel des Copépodes, tel que je l'ai interprété, est relativement simple, caractérisé par une longévité étendue et par une possibilité de ne compenser, qu'à la fin de l'été et en automne, un départ mal réussi au printemps. Les populations de *Bosmina* et de *Daphnia* ont, autant qu'on puisse en juger, plusieurs générations entre la débacle et l'automne. C'est pourquoi ils peuvent plus rapidement compenser un départ de printemps mal réussi (cf. D'ANCONA 1955, p. 44).

L'ontogénèse rapide des *Diaptomus* indique une grande provision de nourriture pour les animaux filtrants dans Ottsjön — lac sans thermocline — et la courbe d'abondance des populations de *Daphnia, Bosmina* et *Diaptomus,* remonte vite. Par la suite vient une phase critique pour ces populations: Des *Daphnia* mâles paraissent au mois de juillet et les trois populations diminuent en abondance, *Diaptomus,* fin juin, les autres, pendant juillet, pour des années normales (Cf. BROWN 1929, p. 446). Selon STUART et alii (1931), BERG (1936) et BANTA et alii (1939), c'est un métabolisme un peu réduit qui conduit à la formation de *Daphnia* mâles, poursuivi il conduit à la formation d'œufs durables. On a observé ces œufs au mois d'août. Il semble donc que c'est le fait d'une densité importante (*crowding*) et non pas la prédation qui décide des traits essentiels dans le cycle annuel pendant cette phase descendante. Les planctons rapaces, *Polyphemus, Bytotrephes* et *Heterocope,* paraissent surtout en juillet et en août, trouvant une nourriture abondante. Le régime des jeunes poissons est peu connu, omble chevalier, truite, vairon, lotte et ombre existent dans ce lac. L'omble chevalier adulte passe au régime plancton surtout au mois d'août (LINDSTRÖM 1955), mais cela n'empèche pas le développement qui mène à la formation d'œufs durables. Cependant une porte s'ouvre qui permet une augmentation de la population *Diaptomus* qui ne sert pas de nourriture à l'omble chevalier. Cela fait penser que les *Diaptomus* et les Cladocères sont en compétition pour la nourriture. La source de ce recrutement des *Diaptomus* n'a pu être décelée (Cf. étude de 1952, p. 98). Les stations auxiliaires ne paraissent pas être des refuges de *Diaptomus.* Mais la seconde hypothèse, présentée en 1952, ne peut être exclue. Il est possible aussi que des *Diaptomus* copépodites âgés reposent sur le fond pendant les périodes de disette.

Dans Hottön et Håckren (réservation voir p. 114), les points culminants des courbes d'abondance de *Bosmina* et *Daphnia* n'ont lieu qu'au mois d'août et jusqu'à cette période le rapport entre l'abondance de nourriture et la croissance des populations de crustacés filtrants doit être assez équilibré. En août a lieu une densité critique (*crowding*), et, conformément à celle-ci, les *Daphnia* mâles paraissent plus tard que dans Ottsjön. On a observé, au mois d'août, des œufs durables, chez les femelles, dans Hottön et Håckren. Le développement des *Diaptomus* est beaucoup plus lent que dans Ottsjön. Les planctons rapaces ne paraissent dans ces lacs qu'en juillet et août. En plus des espèces de poissons mentionnées pour Ottsjön, il faut ajouter le brochet et la perche, tandis que l'omble chevalier, qui se nourrit en grande partie de plancton, se rencontre moins fréquemment que dans Ottsjön. Le déplacement en août du point culminant de la densité des planctons filtrants dans ces lacs de moindre altitude, ne peut s'expliquer par une prédation plus forte en juin-juillet, dans la mesure où les faits connus autorisent l'analyse.

Contrairement au cycle annuel des filtrateurs, celui des *Cyclops,* est plus rapide dans Håckren que dans Ottsjön (fraction A). Les *Cyclops* étant visiblement concentrés dans l'eau froide du fond de Håckren, ce développement plus rapide ne peut guère se rattacher directement à l'effet d'une température plus élevée dans l'épilimnium de Håckren (les migrations diurnes ne sont pas aussi marquantes chez les *Cyclops* que chez les filtrateurs, cf. LINDSTRÖM, 1952, p. 84 et 104, Tab. 9, p. 144, 150, 154). La pulsation des *Cyclops,* au printemps et à la fin de l'été apparaît dans des conditions de température différentes, ce qui indique une certaine indépendance vis à vis de la température. On retrouve aussi, de jour, des *Diaptomus,* concentrés dans l'eau froide du fond de Håckren; mais la température de juin, juillet, n'est pas plus basse ici que celle de Ottsjön, en juin (1957). Il ressort de la discussion précèdente que j'ai abandonné l'hypothèse (Op. cit. p. 99) qu'une différence de température puisse être la cause directe d'une différence entre la vitesse de l'ontogénèse des *Diaptomus* dans Ottsjön et celle des autres lacs. Selon EKMAN (1904), les *Diaptomus laticeps* sont remplacés par les *Diaptomus laciniatus,* dans les lacs dont l'altitude est plus élevée et la température plus basse. (Cf. aussi LINDSTRÖM 1957, Stora Mjölkvattnet.) Quoique les lacs examinés, il n'a pas été obtenu d'épreuves pouvant servir à déterminer que pour des années froides, la courbe d'abondance des *Diaptomus laticeps* serait moins élevée; cependant une faible suggestion demeure (p. 122) qui concorderait avec ce qui précède. De même, pour les *Daphnia* et les *Bosmina* on n'a pas trouvé de différences significatives dans le maximum densité au cours des differents années, quoique les observations pour les *Bosmina* peuvent indiquer une plus grande densité pendant des années froides. Lorsqu'il est question des *Bosmina* il faut cependant tenir compte d'un échange entre le bassin central et les zones littorales du lac (LINDSTRÖM 1957). C'est pourquoi on ne doit tirer de conclusions, sur les changements d'abondance, qu'avec la plus grande circonspection. On peut dire que, si on ne possède pas un matériel très riche, les comparaisons entre les densités qu'on a essayé d'établir ici, à cause de la répartition horizontale irrégulière, du cycle annuel avec ses changements d'abondance rapides (*Cyclops, Diaptomus*), et, des oscillations des populations de Cladocères (SLOBODKIN 1954) ces comparaisons sont d'avance vouées à l'échec. Pourtant l'impression à laquelle on ne peut échapper est qu'il y a peu de différences entre les années.

Dans le paragraphe précédent quelques cas pour lesquels on n'a pu prouver l'effet direct du facteur température sur les différences entre des lacs, ou maxima d'été, ont été réunis. Mais sous un certain rapport il y a concomitance entre l'évolution de la température et le développement des populations de planctons crustacés. La plupart des observations sur les années à débacle tardive et à été froid (1951, 1957), concordent avec la théorie du retardement des cycles annuels des populations pour des années froides et à débacle tardive. Retardement qui s'étend jusqu'en août. (La parution de la pulsation de fin d'été, chez les *Cyclops* copépodites jeunes, fait exception, voir p. 120.) Dans le cas d'un parallèlisme visible, entre les températures de l'année et le cycle annuel des populations, il ne faut pas seulement l'interpréter comme une influence directe de la température sur la rapidité de développement des individus et des populations, cf. le résumé sur la littérature planctonique, p. 128.

La relation entre la densité et la proportion de renouvellement des populations n'a pas été traitée jusqu'à présent. Des auteurs précédents ont signalé, qu'il peut exister parallèlement une densité élevée et une basse proportion de renouvellement par unité de temps. En se rapportant à des observations sur des populations de Cladocères des eaux douces arctiques, POULSEN (1940) et EDMONDSON (1955), pour ne citer que les œuvres les plus récentes, on peut supposer que, dans les lacs du Jämtland, lors d'une année froide, la proportion de renouvellement de la population Cladocères, diminue. Il ne faut pas s'attendre, si mon interprétation du cycle annuel est valable, à une déviation manifeste de la proportion de renouvellement des Copépodes, pendant les mois d'été, que les années soient froides ou chaudes.

Il est évident que les connaissances rudimentaires, au sujet de la rapidité de renouvellement des populations de planctons crustacés, ne sont pas satisfaisantes à bien des points de vue. Certes le cas est spécial pour les prédateurs de fond, qui se tiennent dans l'émissaire, et vivent d'individus planctons, qui malgré leurs mécanismes de défense, sont emportés par l'eau d'écoulement. L'activité de ces prédateurs n'agit pas sur la densité des planctons crustacés contenus dans l'eau du lac. Mais par contre, pour les populations de prédateurs, qui vivent dans le lac, la densité planctonique peut éveiller leur attention sur cette proie signalant qu'il est lucratif, temporairement, de passer au régime plancton. Mais, la possibilité de continuer longtemps ce régime est dépendant de la faculté qu'ont les populations d'animaux servant de proie, à remplir les vides causés par les prédateurs.

Une connaissance plus approfondie, de la vitesse de renouvellement des populations de planctons crustacés, serait aussi à souhaiter, si on veut pouvoir donner une portée plus grande à la notion d'optimum, car on ne peut dire qu'il est correct de définir optimum du seul point de vue de la densité des populations. Une vitesse de renouvellement accélérée doit nécessairement amener une plus grande exigeance des utilités pour lesquelles les populations entrent en compétition.

Conclusions

Dans le Tabl. 7 les différences entre Håckren au cours des années avec une débacle tardive et Ottsjön lors d'une année normale sont traitées avec l'analyse de la variance. Les autres indications contenues dans le matériel permettent une analyse poursuivie mais les resultats sont moins affirmés. Toutes les populations réagissent par un retardement du cycle annuel après une débacle tardive et pendant un été froid (exception, voir p. 120). Les différences entre les lacs amènent les populations des filtrateurs à réagir à l'opposé de la population du *Cyclops*. Des différences entre des lacs avoisinants sont discutées entre autres par LANGFORD (1938), PENNAK (1946, 1949) et TONOLLI (1954). Le dualisme des populations Copépodes contribue à la plasticité des populations, une plasticité qui doit être favorable pour une espèce qui habite des lacs assez différents.

Le dualisme est étudié au printemps et en été. La limite entre différentes familles de Copépodes ne coïncide pas avec la limite entre les façons différentes de démarrer une pulsation de printemps. RAVERA a signalé, en 1955, que dans le groupe Copépode, il y a plusieurs modes de reproduction et de cycles biologiques. Il peut se produire que des espèces proches parentes suivent des modèles différents tandis que des espèces moins apparentées suivent le même modèle. Les différences entre les deux fractions de populations de Copépodes analysées en 1952 et dans les chapitres, qui précèdent, s'adaptent très bien à cette théorie si on ne tient pas compte du fait que ces différences semblent pouvoir être complètement dépendantes du milieu et être provoquées de nouveau chaque hiver.

Summary

The annual cycle of the plankton Crustacea in some Jämtland lakes is investigated. New evidences in favour of the dualism theory are presented. This dualism implies that there are two fractions with different annual cycles in the *Cyclops* and *Diaptomus* populations. The dualism is far from equally evident in all lakes; there is no case of indisputable cohabitation of the two *Diaptomus* fractions in one lake.

The dualism is probably regenerated every winter. One fraction originates from copepodites IV and V — old copepodites function as resting stage with the Copepods. The other fraction originates from resting eggs (*Diaptomus*) or as a spring pulse of nauplii and young copepodites (*Cyclops*). The origin of this nauplii production is not settled. Hypothetical mechanisms for the fusion of the fractions during the summer are discussed.

The comparison between lakes and between years are only supported by analysis of variance up to a certain point (Table 7), but the material contains other kinds of verifications (ontogenetical stage sequences, vertical tow-

net samples, repetition equivalent years). In Lake Håckren the speed of ontogenesis of *Cyclops* (fraction A) is greater than in Lake Ottsjön. In Lakes Håckren and Hottön the speed of ontogenesis of *Diaptomus* up to the adult stage is slower than in Lake Ottsjön. The differences cannot reasonably be directly depending on differences in temperature. Clear differences between maximal densities of plankton Crustacea cold and warm years could not be demonstrated. The paramount importance of the temperature factor is of course not denied, but an effect of the temperature factor could only be demonstrated as a retardment of the annual cycle in years with retarded breaking up of the ice and following cold summer.

There is a difference in the development of the cladocerean populations in different lakes: a maximum density in Lakes Håckren and Hottön is reached later in the summer than in Lake Ottsjön. The rapid development of two cladocerean populations in Lake Ottsjön and the rapid ontogenesis of the population of the third filter feeder (*Diaptomus*) in this unstratified lake and the slow ontogenesis of the particle seizer (*Cyclops*) indicate that food plays an important rôle in the processes discussed, filter feeder depending on the same food pulse. The unsettled assumption is advanced that the filter feeder *Daphnia, Diaptomus* and *Bosmina* compete for food.

The importance of the dualisme of the Copepod populations in diversified environment is discussed.

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TABLEAUX

Tableau 1. Existence de *Diaptomus* copépodites et adultes dans les épreuves à la verticale, prises avec filet dans Ottsjön en 1953. Ouverture de maille du filet: 150 à 200 μ. A cause de la grande ouverture de mailles on a supprimé les renseignements sur les nauplii. Orifice du filet 28 cm.

5.6	Copépodites âgés
9.6	» » et adultes, les femelles sans oeufs
13.6	» » » » » » » »
17.6	Adultes, les femelles sans oeufs
22.6	» » » » »
26.6	» » » » »
30.6	» » » » »
4.7	» » » » »

Tableau 3. Epreuves verticales de 1957 prises avec filet, du fond jusqu'à la surface. Diamètre de l'orifice du filet: 11 cm. Ouverture des mailles: 70 μ Toutes les épreuves ont été prises dans les parties les plus profondes des lacs (station A). Les chiffres indiquent le nombre total d'individus capturés. Dans un plus grand filet qui était traîné plusieurs fois entre le fond et la surface de Håckren, le 8.4.57, ne se trouvait pris aucun *Diaptomus*. Orifice de ce filet 28 cm., ouverture des mailles 140—160 μ.

Lac	HÅCKREN							GESTEN					OTTSJÖN				
Date	8.4	4.6	16.6	3.7	18.7	6.8	31.8	5.6	16.6	3.7	18.7	6.8	5.6	17.6	2.7	18.7	5.8
Heure	11h30	18h	13h	12h	16h	10h	11h	11h30	18h30	10h	18h	13h	17h30	11h30	12h	10h	19h
Profondeur totale en mètres	15	16	17	17	17	17	17	23	23	24	26	$24\frac{1}{2}$	28	28	28	28	27
Nombre d'épreuves entre le fond et la surface	6	1	1	1	1	1	1	1	1	1	1	1	1	1	1 +	1	1
Centropagidae, nauplii	—	13	27	—	—	—	—	5	30	5	1	—	10	1	—	—	—
Diaptomus I—III copépodites	—	—	8	14	11	—	—	1	5	5	7	—	41	—	—	—	—
» IV—V »	—	1	—	1	10	4	—	2	—	—	—	—	6	52	—	—	—
Diaptomus laticeps ♀♀ (* = avec oeufs)	—	—	—	—	—	1	2	—	3*	—	—	—	—	1	3	1+1*	7
» » ♂♂	—	—	—	—	—	—	3	—	1	—	—	1	—	—	1	1	3
Heterocope, adultes ou copépodites	—	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—
Cyclopidae, nauplii	175	6	82	234	278	410	454	1	58	78	20	18	79	12	88	481	670
Cyclops copépodites I—III	25	11	38	6	1	4	120	10	257	10	1	2	149	201	143	7	1
» » IV	6	—	12	4	2	—	6	—	37	2	1	0	5	2	34	71	22
» » V	2	—	1	4	1	—	1	—	1	2	4	4	48	4	1	32	99
Cyclops scutifer ♀♀ avec poche d'oeufs	—	—	—	5	1	—	—	—	4	1	1	2	—	8	10	14	5
» » ♀♀ sans » »	—	—	1	2	1	1	—	—	2	—	—	1	9	32	9	16	16
» » ♂♂	—	1	1	9	2	3	1	—	20	—	1	10	19	22	19	2	7
Daphnia l. hyalina ♀♀ jeunes	—	—	4	1	6	2	35	—	11	—	—	23	5	1	25	39	73
» » » ♀♀ adultes	—	—	—	—	2	2	26	—	17	—	2	14	—	7	2	9	63
» » » ♂♂	—	—	—	—	—	1	70	—	—	—	—	8	—	—	—	2	22
Bosmina coregoni ♀♀	—	1	3	—	25	9	121	—	40	23	56	347	10	7	75	62	132
Holopedium gibberum	—	—	—	—	—	—	—	—	6	—	—	—	6	14	—	11	9
Polyphemus pediculus	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—
Autres espèces de cladocères	—	—	—	—	—	—	—	1	12	—	—	—	1	1	—	—	—

Tableau 2. Somme des individus — S(x) — pour le nombre d'épreuves indiqué dans chaque colonne. Somme du (nombre par épreuve)^2 — $S(x^2)$. Les épreuves sont prises avec le chercheur de planctons. Les stations et les profondeurs totales peuvent être trouvées dans le travail de 1952. Le volume d'épreuves est partout de 5,3 litres. Les épreuves F sont prises à 1 m. environ du fond. La plupart des Centropagidae, nauplii sont sans doute *Diaptomus*. En ce qui concerne la nomenclature, pour être en conformité avec certains systématiciens, il faudrait remplacer «Centropagidae» par «Calanoida».

Lac, station	HÅCKREN, A									
	Date 31.5.55 Heure 13h30—16h									
Prof. d'épreuves en mètres	0		2		5		10		F	
Nombre d'épreuves	3		3		3		3		3	
	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$
Centropagidae, nauplii	—	—	—	—	1	1	1	1	4	6
Diaptomus copépodites	—	—	—	—	—	—	—	—	—	—
Diaptomus laticeps ♀♀ (x=avec œufs)	—	—	—	—	—	—	—	—	—	—
» » ♂♂	—	—	—	—	—	—	—	—	—	—
Heterocope, adultes ou copépodites	—	—	—	—	—	—	—	—	—	—
Cyclopidae nauplii	—	—	1	1	1	1	2	4	1	1
Cyclops copépodites I—III	—	—	—	—	—	—	1	1	1	1
» » IV	—	—	—	—	—	—	—	—	2	4
» » V	—	—	—	—	—	—	—	—	—	—
» scutifer ♀♀ avec poche d'œufs	—	—	—	—	—	—	—	—	—	—
» » ♀♀ sans » »	—	—	—	—	—	—	—	—	—	—
» » ♂♂	—	—	—	—	—	—	—	—	—	—
Daphnia l. hyalina ♀♀ jeunes	—	—	—	—	1	1	—	—	—	—
» » ♀♀ adultes	—	—	—	—	—	—	—	—	—	—
» » ♂♂	—	—	—	—	—	—	—	—	—	—
Bosmina coregoni ♀♀	1	1	—	—	—	—	—	—	—	—
Holopedium gibberum	—	—	—	—	—	—	—	—	—	—
Polyphemus pediculus	—	—	—	—	—	—	—	—	—	—
Autres espèces de Cladocères	—	—	—	—	—	—	—	—	—	—

Lac, station	HÅCKREN, A									
	Date 8.6.55 Heure 12h30—15h									
Prof. d'épreuves en mètres	0		2		5		10		F	
Nombre d'épreuves	3		3		3		3		3	
	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$
Centropagidae, nauplii	1	1	—	—	—	—	3	5	23	259
Diaptomus copépodites	—	—	—	—	—	—	—	—	—	—
Diaptomus laticeps ♀♀ (x=avec œufs)	—	—	—	—	—	—	—	—	—	—
» » ♂♂	—	—	—	—	—	—	—	—	—	—
Heterocope, adultes ou copépodites	—	—	—	—	—	—	—	—	—	—
Cyclopidae nauplii	—	—	—	—	—	—	2	4	15	113
Cyclops copépodites I—III	—	—	—	—	—	—	2	4	52	1002
» » IV	—	—	—	—	—	—	—	—	5	13
» » V	—	—	—	—	—	—	—	—	—	—
» scutifer ♀♀ avec poche d'œufs	—	—	—	—	—	—	—	—	—	—
» » ♀♀ sans » »	—	—	—	—	—	—	—	—	—	—
» » ♂♂	—	—	—	—	—	—	—	—	2	4
Daphnia l. hyalina ♀♀ jeunes	4	16	1	1	—	—	1	1	1	1
» » ♀♀ adultes	1	1	—	—	3	5	—	—	2	2
» » ♂♂	—	—	—	—	—	—	—	—	—	—
Bosmina coregoni ♀♀	—	—	—	—	—	—	—	—	3	5
Holopedium gibberum	—	—	—	—	—	—	—	—	—	—
Polyphemus pediculus	—	—	—	—	—	—	—	—	—	—
Autres espèces de Cladocères	—	—	—	—	—	—	—	—	—	—

Lac, station	HÅCKREN, A									
	Date 22.6.55 Heure 11h—13h									
Prof. d'épreuves en mètres	0		2		5		10		F	
Nombre d'épreuves	3		3		3		3		3	
	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$
Centropagidae, nauplii	3	3	1	1	7	17	1	1	2	2
Diaptomus copépodites	—	—	1	1	—	—	—	—	2	4
Diaptomus laticeps ♀♀ (x=avec œufs)	—	—	—	—	—	—	—	—	—	—
» » ♂♂	—	—	—	—	—	—	—	—	—	—
Heterocope, adultes ou copépodites	—	—	—	—	—	—	—	—	—	—
Cyclopidae nauplii	1	1	—	—	1	1	—	—	59	1729
Cyclops copépodites I—III	—	—	1	1	1	1	1	1	35	507
» » IV	—	—	} 1	1 {	—	—	—	—	5	17
» » V	—	—			—	—	1	1	5	9
» scutifer ♀♀ avec poche d'œufs	1	1	—	—	—	—	—	—	—	—
» » ♀♀ sans » »	—	—	—	—	—	—	1	1	5	13
» » ♂♂	—	—	—	—	—	—	1	1	9	45
Daphnia l. hyalina ♀♀ jeunes	5	17	23	201	24	192	8	64	1	1
» » ♀♀ adultes	4	8	16	126	16	118	4	10	1	1
» » ♂♂	—	—	—	—	—	—	—	—	—	—
Bosmina coregoni ♀♀	—	—	—	—	—	—	1	1	2	2
Holopedium gibberum	—	—	—	—	—	—	—	—	—	—
Polyphemus pediculus	—	—	—	—	—	—	—	—	—	—
Autres espèces de Cladocères	—	—	—	—	—	—	—	—	—	—

Lac, station	HÅCKREN, A									
	Date 3.7.55 Heure 12h—14h									
Prof. d'épreuves en mètres	0		2		5		10		F	
Nombre d'épreuves	3		3		3		3		3	
	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$
Centropagidae, nauplii	1	1	1	1	—	—	—	—	8	30
Diaptomus copépodites	—	—	2	4	—	—	—	—	—	—
Diaptomus laticeps ♀♀ (x=avec œufs)	—	—	—	—	—	—	—	—	—	—
» » ♂♂	—	—	—	—	—	—	1	1	—	—
Heterocope, adultes ou copépodites	—	—	—	—	—	—	—	—	—	—
Cyclopidae nauplii	—	—	—	—	—	—	1	1	284	53994
Cyclops copépodites I—III	—	—	1	1	1	1	—	—	9	27
» » IV	—	—	1	1	1	1	2	2	2	2
» » V	—	—	1	1	—	—	4	8	1	1
» scutifer ♀♀ avec poche d'œufs	—	—	—	—	—	—	—	—	1	1
» » ♀♀ sans » »	—	—	—	—	—	—	3	5	3	3
» » ♂♂	—	—	2	2	—	—	5	13	5	11
Daphnia l. hyalina ♀♀ jeunes	2	4	29	365	14	74	2	4	—	—
» » ♀♀ adultes	3	5	68	1686	78	2486	15	99	—	—
» » ♂♂	—	—	—	—	—	—	—	—	—	—
Bosmina coregoni ♀♀	1	1	—	—	3	5	5	11	1	1
Holopedium gibberum	—	—	—	—	—	—	1	1	1	1
Polyphemus pediculus	—	—	—	—	—	—	—	—	—	—
Autres espèces de Cladocères	—	—	—	—	—	—	—	—	3	9

Lac, station	HÅCKREN, A									
	Date 13.7.55 Heure 11h—13h									
Prof. d'épreuves en mètres	0		2		5		10		F	
Nombre d'épreuves	3		3		3		3		3	
	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$
Centropagidae, nauplii	—	—	—	—	—	—	—	—	12	56
Diaptomus copépodites	—	—	—	—	—	—	1	1	5	9
Diaptomus laticeps ♀♀ (x=avec œufs)	—	—	—	—	—	—	—	—	—	—
» » ♂♂	—	—	—	—	—	—	—	—	—	—
Heterocope, adultes ou copépodites	—	—	—	—	—	—	—	—	—	—
Cyclopidae nauplii	—	—	—	—	—	—	—	—	95	3449
Cyclops copépodites I—III	—	—	—	—	—	—	—	—	—	—
» » IV	—	—	—	—	—	—	—	—	—	—
» » V	—	—	—	—	—	—	—	—	—	—
» scutifer ♀♀ avec poche d'œufs	—	—	—	—	—	—	—	—	1	1
» » ♀♀ sans » »	—	—	—	—	—	—	—	—	—	—
» » ♂♂	—	—	—	—	—	—	—	—	—	—
Daphnia l. hyalina ♀♀ jeunes	1	1	2	2	41	621	1	1	1	1
» » ♀♀ adultes	—	—	—	—	2	2	—	—	1	1
» » ♂♂	—	—	—	—	—	—	—	—	—	—
Bosmina coregoni ♀♀	1	1	4	6	5	11	1	1	—	—
Holopedium gibberum	—	—	—	—	—	—	—	—	—	—
Polyphemus pediculus	—	—	—	—	—	—	—	—	—	—
Autres espèces de Cladocères	—	—	—	—	—	—	—	—	—	—

Lac, station	HÅCKREN, A									
	Date 12.8.55 (13.8) Heure 11h30—12h30									
Prof. d'épreuves en mètres	0		2		5		10		F	
Nombre d'épreuves	3		3		3		3		3	
	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$
Centropagidae, nauplii	—	—	—	—	—	—	—	—	—	—
Diaptomus copépodites	2	2	1	1	—	—	—	—	6	36
Diaptomus laticeps ♀♀ (x=avec œufs)	—	—	—	—	—	—	—	—	—	—
» » ♂♂	—	—	—	—	—	—	—	—	—	—
Heterocope, adultes ou copépodites	—	—	—	—	—	—	—	—	—	—
Cyclopidae nauplii	—	—	—	—	2	2	94	3604	575	123597
Cyclops copépodites I—III	—	—	1	1	—	—	3	3	5	11
» » IV	—	—	—	—	—	—	—	—	—	—
» » V	—	—	—	—	—	—	—	—	—	—
» scutifer ♀♀ avec poche d'œufs	—	—	—	—	—	—	1	1	—	—
» » ♀♀ sans » »	—	—	—	—	—	—	—	—	—	—
» » ♂♂	—	—	—	—	—	—	—	—	4	10
Daphnia l. hyalina ♀♀ jeunes	—	—	4	6	7	29	21	365	77	2197
» » ♀♀ adultes	1	1	452	80318	430	75922	4	10	8	34
» » ♂♂	—	—	4	16	5	13	8	50	42	630
Bosmina coregoni ♀♀	—	—	2	4	2	2	1	1	55	1717
Holopedium gibberum	—	—	—	—	—	—	—	—	—	—
Polyphemus pediculus	8	40	—	—	—	—	1	1	—	—
Autres espèces de Cladocères	—	—	—	—	—	—	—	—	—	—

Lac, station	HÅCKREN, A									
	Date 4.6.57 Heure 17h—18h									
Prof. d'épreuves en mètres	0		2		5		10		F	
Nombre d'épreuves	3		3		3		3		3	
	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$
Centropagidae, nauplii	—	—	—	—	4	10	1	1	36	528
Diaptomus copépodites	—	—	—	—	—	—	—	—	—	—
Diaptomus laticeps ♀♀ (x=avec œufs)	—	—	—	—	—	—	—	—	—	—
» » ♂♂	—	—	—	—	—	—	—	—	—	—
Heterocope, adultes ou copépodites	—	—	—	—	—	—	—	—	—	—
Cyclopidae nauplii	—	—	1	1	—	—	4	10	26	330
Cyclops copépodites I—III	—	—	—	—	1	1	4	16	21	173
» » IV	—	—	—	—	1	1	—	—	—	—
» » V	—	—	—	—	—	—	—	—	—	—
» scutifer ♀♀ avec poche d'œufs	—	—	—	—	—	—	—	—	1	1
» » ♀♀ sans » »	—	—	—	—	—	—	—	—	—	—
» » ♂♂	—	—	—	—	1	1	—	—	2	4
Daphnia l. hyalina ♀♀ jeunes	—	—	—	—	—	—	—	—	—	—
» » ♀♀ adultes	—	—	—	—	—	—	—	—	—	—
» » ♂♂	—	—	—	—	—	—	—	—	—	—
Bosmina coregoni ♀♀	—	—	—	—	1	1	—	—	2	2
Holopedium gibberum	—	—	—	—	—	—	—	—	—	—
Polyphemus pediculus	—	—	—	—	—	—	—	—	—	—
Autres espèces de Cladocères	2	4	—	—	1	1	—	—	—	—

Lac, station	HÅCKREN, A									
	Date 16.6.57 Heure 13h—14h30									
Prof. d'épreuves en mètres	0		2		5		10		F	
Nombre d'épreuves	3		3		3		3		3	
	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$
Centropagidae, nauplii	1	1	2	4	3	5	—	—	26	230
Diaptomus copépodites	—	—	—	—	—	—	—	—	2	4
Diaptomus laticeps ♀♀ (x=avec œufs)	—	—	—	—	—	—	—	—	—	—
» » ♂♂	—	—	—	—	—	—	—	—	—	—
Heterocope, adultes ou copépodites	1	1	1	1	1	1	—	—	—	—
Cyclopidae nauplii	—	—	—	—	1	1	2	4	31	333
Cyclops copépodites I—III	—	—	2	2	20	186	3	5	31	355
» » IV	—	—	—	—	6	14	5	9	2	2
» » V	—	—	1	1	1	1	—	—	—	—
» scutifer ♀♀ avec poche d'œufs	—	—	—	—	—	—	1	1	—	—
» » ♀♀ sans » »	—	—	2	2	—	—	—	—	1	1
» » ♂♂	—	—	1	1	—	—	1	1	1	1
Daphnia l. hyalina ♀♀ jeunes	10	36	6	26	10	54	—	—	—	—
» » ♀♀ adultes	—	—	2	2	1	1	—	—	—	—
» » ♂♂	—	—	—	—	—	—	—	—	—	—
Bosmina coregoni ♀♀	2	4	3	3	1	1	4	8	—	—
Holopedium gibberum	—	—	—	—	—	—	—	—	1	1
Polyphemus pediculus	—	—	—	—	—	—	—	—	—	—
Autres espèces de Cladocères	1	1	—	—	—	—	—	—	1	1

Lac, station	HÅCKREN, A									
	Date 3.7.57 Heure 12h—14h									
Prof. d'épreuves en mètres	0		2		5		10		F	
Nombre d'épreuves	3		3		3		3		3	
	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$
Centropagidae, nauplii	—	—	—	—	—	—	—	—	3	9
Diaptomus copépodites	—	—	—	—	—	—	3	5	85	2421
Diaptomus laticeps ♀♀ (x=avec œufs)	—	—	—	—	—	—	—	—	—	—
» » ♂♂	—	—	—	—	—	—	—	—	—	—
Heterocope, adultes ou copépodites	—	—	—	—	—	—	—	—	—	—
Cyclopidae nauplii	1	1	2	4	—	—	12	54	196	13776
Cyclops copépodites I—III	—	—	—	—	—	—	1	1	5	13
» » IV	—	—	—	—	—	—	—	—	13	85
» » V	—	—	—	—	—	—	3	3	4	16
» scutifer ♀♀ avec poche d'œufs	—	—	—	—	—	—	4	6	1	1
» » ♀♀ sans » »	—	—	—	—	—	—	1	1	—	—
» » ♂♂	—	—	—	—	—	—	2	4	10	34
Daphnia l. hyalina ♀♀ jeunes	4	6	—	—	1	1	—	—	—	—
» » ♀♀ adultes	—	—	—	—	—	—	—	—	—	—
» » ♂♂	—	—	—	—	—	—	—	—	—	—
Bosmina coregoni ♀♀	3	9	—	—	1	1	1	1	—	—
Holopedium gibberum	—	—	—	—	—	—	—	—	—	—
Polyphemus pediculus	—	—	—	—	—	—	—	—	—	—
Autres espèces de Cladocères	—	—	—	—	—	—	—	—	—	—

Lac, station	HÅCKREN, A									
	Date 18.7.57 Heure 15h—16h30									
Prof. d'épreuves en mètres	0		2		5		10		F	
Nombre d'épreuves	3		3		3		3		3	
	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$
Centropagidae, nauplii	—	—	—	—	—	—	—	—	—	—
Diaptomus copépodites	—	—	—	—	—	—	2	4	42	770
Diaptomus laticeps ♀♀ (x=avec œufs)	—	—	—	—	—	—	—	—	—	—
» » ♂♂	—	—	—	—	—	—	—	—	—	—
Heterocope, adultes ou copépodites	—	—	—	—	—	—	—	—	—	—
Cyclopidae nauplii	—	—	—	—	—	—	120	5522	243	22577
Cyclops copépodites I—III	1	1	—	—	—	—	2	2	—	—
» » IV	—	—	—	—	—	—	1	1	—	—
» » V	—	—	—	—	—	—	4	6	1	1
» scutifer ♀♀ avec poche d'œufs	—	—	—	—	—	—	2	4	—	—
» » ♀♀ sans » »	—	—	1	1	1	1	1	1	—	—
» » ♂♂	—	—	—	—	—	—	2	2	—	—
Daphnia l. hyalina ♀♀ jeunes	1	1	5	17	15	83	—	—	1	1
» » ♀♀ adultes	—	—	5	17	6	26	—	—	—	—
» » ♂♂	—	—	—	—	—	—	—	—	—	—
Bosmina coregoni ♀♀	3	5	10	36	56	1210	10	46	—	—
Holopedium gibberum	—	—	—	—	—	—	—	—	—	—
Polyphemus pediculus	1	1	—	—	—	—	—	—	—	—
Autres espèces de Cladocères	—	—	—	—	—	—	—	—	—	—

Lac, station	HÅCKREN, A									
	Date 6.8.57 Heure 10h—12h									
Prof. d'épreuves en mètres	0		2		5		10		F	
Nombre d'épreuves	3		3		3		3		3	
	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$
Centropagidae, nauplii	—	—	—	—	—	—	—	—	—	—
Diaptomus copépodites	—	—	—	—	—	—	—	—	17	117
Diaptomus laticeps ♀♀ (x=avec œufs)	—	—	—	—	—	—	—	—	1	1
» » ♂♂	—	—	—	—	—	—	—	—	1	1
Heterocope, adultes ou copépodites	—	—	—	—	—	—	—	—	—	—
Cyclopidae nauplii	—	—	—	—	3	3	24	254	499	88843
Cyclops copépodites I—III	—	—	—	—	—	—	1	1	—	—
» » IV	—	—	—	—	—	—	—	—	—	—
» » V	—	—	—	—	—	—	—	—	—	—
» scutifer ♀♀ avec poche d'œufs	—	—	—	—	—	—	—	—	—	—
» » ♀♀ sans » »	—	—	—	—	—	—	—	—	—	—
» » ♂♂	—	—	—	—	—	—	1	1	6	26
Daphnia l. hyalina ♀♀ jeunes	—	—	—	—	1	1	—	—	—	—
» » ♀♀ adultes	—	—	1	1	7	21	1	1	—	—
» » ♂♂	—	—	—	—	1	1	—	—	1	1
Bosmina coregoni ♀♀	—	—	6	20	4	8	8	30	1	1
Holopedium gibberum	—	—	—	—	—	—	—	—	—	—
Polyphemus pediculus	9	81	2	4	1	1	—	—	—	—
Autres espèces de Cladocères	—	—	—	—	—	—	—	—	—	—

Lac, station	HOTTÖN, A	
	Date 2—3.8.54 Heure 23h20—0h40	
Prof. d'épreuves en mètres	0	
Nombre d'épreuves	21	
	S(x)	$S(x^2)$
Centropagidae, nauplii	—	—
Diaptomus copépodites	424	10520
Diaptomus laticeps ♀♀ (x=avec œufs)	3	3
» » ♂♂	1	1
Heterocope, adultes ou copépodites	1	1
Cyclopidae nauplii	5	7
Cyclops copépodites I—III	—	—
» » IV	} 95	963 {
» » V		
» scutifer ♀♀ avec poche d'œufs	13	137
» » ♀♀ sans » »	66	442
» » ♂♂	68	450
Daphnia l. hyalina ♀♀ jeunes	1838	182992
» » ♀♀ adultes	172	1796
» » ♂♂	800	36258
Bosmina coregoni ♀♀	9347	9985035
Holopedium gibberum	—	—
Polyphemus pediculus	—	—
Autres espèces de Cladocères	2	2
	1 naupl. + 2 copédites d'une espèce non identifiée	

Lac, station	OTTSJÖN, A											
	Date 27.5.55 Heure 11h45—14h30											
Prof. d'épreuves en mètres	½		5		10		15		20		F	
Nombre d'épreuves	3		3		3		3		3		3	
	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$
Centropagidae, nauplii	1	1	1	1	1	1	2	2	1	1	—	—
Diaptomus copépodites	5	11	5	17	5	13	6	18	12	62	2	2
Diaptomus laticeps ♀♀ (x=avec œufs)	—	—	—	—	—	—	—	—	—	—	—	—
» » ♂♂	—	—	—	—	—	—	—	—	—	—	—	—
Heterocope, adultes ou copépodites	—	—	—	—	—	—	—	—	—	—	—	—
Cyclopidae nauplii	42	782	33	461	42	1004	60	1418	59	1465	15	81
Cyclops copépodites I—III	1	1	4	10	—	—	1	1	1	1	—	—
» » IV	—	—	4	8	5	9	15	83	7	17	6	18
» » V	2	2	5	13	12	50	6	20	6	14	4	6
» scutifer ♀♀ avec poche d'œufs	—	—	—	—	—	—	—	—	—	—	—	—
» » ♀♀ sans » »	—	—	—	—	—	—	—	—	—	—	—	—
» » ♂♂	—	—	—	—	—	—	—	—	—	—	—	—
Daphnia l. hyalina ♀♀ jeunes	—	—	—	—	—	—	1	1	2	2	—	—
» » ♀♀ adultes	—	—	—	—	—	—	—	—	—	—	—	—
» » ♂♂	—	—	—	—	—	—	—	—	—	—	—	—
Bosmina coregoni ♀♀	—	—	3	5	2	2	—	—	—	—	—	—
Holopedium gibberum	—	—	—	—	—	—	—	—	—	—	—	—
Polyphemus pediculus	—	—	—	—	—	—	—	—	—	—	—	—
Autres espèces de Cladocères	—	—	—	—	—	—	—	—	—	—	—	—

Lac, station	OTTSJÖN, A, C, D													
	Date 5.8.57 Heure 16h—19h													
Prof. d'épreuves en mètres	0		2		5		10		15		20		F	
Nombre d'épreuves	3		3		3		3		3		3		3	
	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$	S(x)	$S(x^2)$
Centropagidae, nauplii	—	—	—	—	1	1	—	—	—	—	—	—	—	—
Diaptomus copépodites	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Diaptomus laticeps ♀♀ (x=avec œufs)	1	1	1	1	—	—	1	1	2	2	1	1	1	1
» » ♂♂	—	—	—	—	—	—	—	—	—	—	1	1	1	1
Heterocope, adultes ou copépodites	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cyclopidae nauplii	100	3742	141	7569	386	53934	182	11372	101	3405	153	9149	141	7301
Cyclops copépodites I—III	—	—	1	1	—	—	—	—	—	—	1	1	3	5
» » IV	—	—	3	9	8	24	4	10	—	—	—	—	8	40
» » V	3	5	79	2325	106	3798	16	134	9	29	4	8	2	2
» scutifer ♀♀ avec poche d'œufs	—	—	—	—	—	—	3	5	—	—	4	10	4	10
» » ♀♀ sans » »	—	—	1	1	—	—	6	14	2	4	5	13	5	11
» » ♂♂	—	—	1	1	1	1	4	6	6	20	11	69	5	17
Daphnia l. hyalina ♀♀ jeunes	—	—	12	62	9	29	2	4	8	38	51	1035	6	14
» » ♀♀ adultes	3	5	51	909	70	1666	4	10	1	1	1	1	1	1
» » ♂♂	2	2	5	13	1	1	—	—	1	1	17	149	11	49
Bosmina coregoni ♀♀	4	10	32	416	5	17	2	2	19	213	58	1636	108	7422
Holopedium gibberum	9	41	6	26	4	16	2	2	—	—	—	—	—	—
Polyphemus pediculus	1	1	—	—	—	—	—	—	—	—	—	—	—	—
Autres espèces de Cladocères	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Lac, station	ÅNN, environ à 2 km au nord de D	
	Date 16,18.8.55 Heure 14h, 17h30, 20h30, 23h	
Prof. d'épreuves en mètres	2—3 (prof. totale 5 m.)	
Nombre d'épreuves	20	
	S(x)	$S(x^2)$
Centropagidae, nauplii	1	1
Diaptomus copépodites	—	—
Diaptomus laticeps ♀♀ (x=avec œufs)	—	—
» » ♂♂	—	—
Heterocope, adultes ou copépodites	13	23
Cyclopidae nauplii	72	610
Cyclops copépodites I—III	—	—
» » IV	} 3	3
» » V		
» scutifer ♀♀ avec poche d'œufs	4	6
» » ♀♀ sans » »	19	43
» » ♂♂	1	1
Daphnia l. hyalina ♀♀ jeunes	19	35
» » ♀♀ adultes	77	619
» » ♂♂	—	—
Bosmina coregoni ♀♀	264	4464
Holopedium gibberum	12	36
Polyphemus pediculus	1	1
Autres espèces de Cladocères	1	1

Tableau 4. Pourcentage de *Daphnia* mâles et de jeunes femelles dans Håckren et Ottsjön. Toutes les épreuves des stations mentionées sont comprises dans l'élaboration du tableau, sauf les épreuves de 2 m. dans Ottsjön. Dans Ottsjön où il y a des épreuves de 2 m., ces épreuves sont inclues dans le calcul des chiffres entre parenthèse. Le nombre d'œufs par femelles portant des œufs dans leur chambre incubatrice descend vers deux, en août, dans tous les lacs. Seules les années 1951, 1955 et 1957 peuvent servir pour une comparaison entre les lacs. Cf. aussi tab. 3.

Lac	Date	Station	Nombre d'épreuves	♂♂	♀♀ jeunes	♀♀ adultes	% ♂♂	% ♀♀ jeunes
Håckren	3.7.55	A	15	0	47	164	0	62
	13.7.55	»	15	0	46	3		
	3.7.57	»	15	0	5	0		
	18.7.57	»	15	0	22	11		
	5.8.51	»	15	0	195	13		
	6.8.57	»	15	2	1	9	7	20
	12.8.55	»	15	59	109	895		
	17.8.51	»	15	38	185	152		
Ottsjön	4—5.7.50	A	30	2	96	79	3	61
	4—5.7.50	E, M	10	2	32	12		
	15.7.50	A	18	0	34	6		
	23.7.50	»	6	1	15	3		
	23.7.50	E	5	5	16	4		
	28.7.50	N	4	1	1	8		
	5.8.57	A, C, D	18	32	76	80	17 (14)	40 (34)
	14.8.50	A	18	9	18	30	19 (17)	28 (20)
	15.8.50	M, N	9	2	0	14		
	17.8.50	A	12	2	1	11		
	17.8.50	E	8	2	15	16		
	22.8.50	A, C, D	18	10	19	25		
	25.8.50	A	7	11	13	14		
	26.8.50	A—D	25	9	3	25		
	28.8.50	D	6	3	4	7		
	30.8.50	C	6	8	7	11		
	11.8.51	A, C, D	17	11	31	16	13 (11)	48 (42)
	20.8.51	»	18	0	9	17		

Tableau 5. Dates de débacle selon l'Institut Suèdois de Météorologie et d'Hydrologie. On appelle jour de débacle celui où le lac ne porte plus de glace, c.a.d. le point final de la débacle pris dans une conception large. En matière de comparaison on a indiqué selon la même source, la date de débacle de certaines sections de la partie ouest de Hottön, et dans l'endroit le plus étroit au milieu de Gesten et de Håckren, colonne S.

Lac	Ottsjön	Hottön		Gesten		Håckren	
Année			S		S		S
1946	7 á 11.5	19.5	—	—	—	—	—
1947	21.5	24.5	—	—	—	—	—
1948	27.4	—	—	—	—	—	—
1949	11.5	Autour du 5.5	5.5	Autour du 4.5	2.5	—	—
1950	11.5	15.5	12.5	» 12.5	8.5	—	—
1951	30.5	29.5	21.5	25.5	18.5	22.5	—
1952	13.5	13.5	5.5	10.5	27.4	8.5	29.4
1953	7.5	11.5	26.4	10.5	19.4	9.5	4.4
1954	24.5	24.5	15.5	22.5	12.5	20.5	11.5
1955	6.6	4.6	27.5	1.6	22.5	30.5	24.5
1956	22.5	19.5	—	17.5	—	15.5	—
1957	27.5	—	—	23.5	—	21.5	—

Tableau 6. Ottsjön. Comparaison entre la densité de *Diaptomus* adultes et *Bosmina,* en juin-juillet 1950, année normale, et août 1951 et 1957, années froides. — Moyennes pour les chiffres présentés dans les Graph. 3 et 11.

Diaptomus adultes		*Bosmina*		
Dates	$\bar{x}$	Dates	$\bar{x}$	
4—5.7 1950	0,55	10.6, 15.6, 4—5.7 1950	5,3	$p = 0,2 - 0,3$
5.8 1957, 11.8 1951	0,57	5.8 1957, 11.8 1951	7,1	

Tableau 7. Cycle annuel—traitement statistique. Valeurs des stations centrales. Les moyennes construites pour les graphiques (p. 100) sont traitées avec analyse de la variance. Pour juger la valeur significative de certaines differences discutées dans le texte, il faut tenir compte du fait que le changement d'abondance pour *Daphnia, Bosmina* et *Diaptomus* cop. dans Håckren est contraire à celui de Ottsjön.

Lac	Forme planctonique	Dates	Changement d'abondance	p
Håckren	Daphnia	3, 13.7 1955, 3, 18.7 1957 5, 17.8 1951, 12.8 1955, 6.8 1957	augmente	0,2
	Bosmina	22.6, 3, 13.7 1955 16.6, 3.7 1957 5, 17.8 1951, 12.8 1955, 6.8 1957	augmente	0,2—0,3
	Diaptomus cop.	31.5, 8, 22.6 1955, 4, 16.6 1957 3, 13.7 1955, 3, 18.7 1957	augmente	0,2—0,05
	Cyclops cop. jeunes	31.5 1955, 4.6 1957 8, 22.6 1955, 16,6 1957 3, 13.7, 12.8 1955, 3, 18.7, 6.8 1951	culmine	0,001
	Cyclops cop. âgés	31.5, 8.6 1955, 4.6 1957 22.6, 3.7 1955, 16.6, 3.7 1957 13.7, 12.8 1955, 18.7, 6.8 1957	culmine	0,01—0,001
Ottsjön	Daphnia	4, 5.7 1950 15, 23.7, 14, 17.8 1950	diminue	0,05—0,01
	Bosmina	10, 15.6, 4, 5.7 1950 15, 23.7, 14, 17.8 1950	diminue	0,05—0,01
	Diaptomus cop.	12, 26, 27.5, 10, 15.6 1950 4, 5, 15, 23.7 1950	diminue	0,005—0.001
	Diapt ad.	Voir le travail 1952, p 90		
	Cyclops	Voir le travail 1952, p 91		

On the Food Competition between two Species of *Coregonus* in a North-Swedish Lake

By **Nils-Arvid Nilsson**

Contents

1. Introduction

Through a series of papers (1949, 1950, 1951, 1952, 1953, 1954 and 1957) SVÄRDSON has in the light of the modern theory of speciation (MAYR 1942) arrived at the conclusion that there exist in the Palaearctic seven species of *Coregonus* which, though very variable in size and other morphological features, have one phenotypically invariable morphological character that makes it possible statistically to distinguish the species from each other: the number of their gillrakers. SVÄRDSON has also pointed out significant differences in the ecology of these species, and proved the occurrence of introgressive hybridization between them; the *Coregonus*-species examplify a "speciation in regress", where the morphological characters have largely disappeared, whereas the ecological characters, standing, as they do, under a stronger selection pressure remained (SVÄRDSON 1958 a, b).

When two or more of the *Coregonus*-species are living sympatrically they characteristically display a marked difference in growth rate with a different size distribution as result. In Lake Vojmsjön in southern Swedish Lapland, for example, there live three species of *Coregonus, C. pidschian* (GMELIN)[1] with roughly 20 gillrakers occurring in all the lake, *C. oxyrhynchus* (LINNAEUS) with roughly 40 gillrakers occurring in the northern part of the lake, and *C. peled* (GMELIN) with roughly 45 gillrakers occurring in all the lake (SVÄRDSON 1957). In the northern part of the lake they form a hybrid population. In Vojmsjön *Oxyrhynchus* is extremely dwarfed (three years old and ripe, when ten centimetres long), *peled* medium-sized, and *pidschian* big (cf. Diagram, Fig. 1). As to the biological significance of the differences in growth rate SVÄRDSON (1954) has explained it to be a result of the consumption of food particles of different size, implying differences

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[1] Latin names after SVÄRDSON (1957).

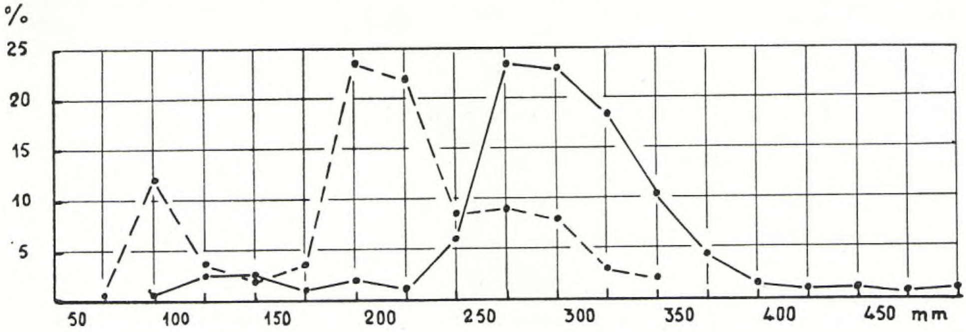

Fig. 1. The size distribution of *Coregonus peled* (- - -) and *pidschian* (——) in Lake Vojmsjön.

in ecology necessary for the species to be able to live side by side without severe competition. The growth rate is also on the whole correlated to the number of gillrakers in such a way that on an average populations with few gillrakers display a better growth than populations with numerous gillrakers (SVÄRDSON 1952).

It is an old idea that the number of gillrakers is correlated with the feeding habits of the whitefish. In Swedish literature we find it already in the work of LILLJEBORG (1891). LILLJEBORG states that *Coregonus*-forms with long and numerous gillrakers consume mainly *Entomostraca,* forms with short and few gillrakers mainly bigger food objects. It has, however, been pointed out by several authors (for example THIENEMANN 1912, MANNSFELD 1930, WIESE 1935, LENZ 1948, 1954, WILLER 1949 and SVÄRDSON 1950) that this rule is not without exceptions: if grown up to a certain size also whitefish with numerous gillrakers consume bigger food objects.

LINDSTRÖM (1955) who studied the feeding habits of the fry of three different whitefish-species in the lakes Uddjaur and Storavan, found that all three species had consumed almost the same food (mostly *Bosmina*), which may indicate that the behaviour mechanism involving a choice of food (the fundament of the formation of food niches) is not fully developed before the fish has reached the adult stage (cf. NILSSON 1957, KALLEBERG 1958). Other isolating mechanisms than differences in feeding habits may in that case be at work in the younger stages (cf. KALLEBERG 1958).

The investigations into feeding habits of adult whitefish underlying the ideas mentioned above have on the whole been rather superficial, intended only as a contribution to the taxonomic work. Hence it is reasonable to re-discuss the problem on the basis of a greater material. The present material was in part sampled by Dr. E. FABRICIUS during 1949—1951 in the northern part of Lake Vojmsjön in connection with his studies of the spawning habits of the fish (FABRICIUS 1950). When the sampling started again in 1954 it was located in the southern part of the lake in order to ascertain a pure material without hybrids. The material from 1949—1951 is thus not directly comparable with that from 1954—1955, particularly as in the meantime the lake was subjected to a regulation of the water-level that certainly affected the composition of the prey fauna of the lake. Altogether 1,126 *Coregonus pidschian* and 430 *C. peled* were examined. The counting of gillrakers and routine examination of the stomach contents was carried out by Mrs. HELVE TOOTS and Mr. OLLE BERGMAN, the critical identifications by the present author.

2. Variations in the feeding habits of the fish

Before the main problem of this investigation is treated, the great variation in the material must first be mentioned. Besides the random variation that characterizes all biological material, the feeding habits of a fish species varies spatially as a response to the prey fauna and the food competitors within the actual environment, and temporarily as a response to the age of the fish and the seasonal and annual fluctuations in the abundance and availability of the prey fauna. The feeding activity of the fish varies also temporarily, the intensity of the feeding being correlated to optimal temperatures and other environmental or innate factors.

Figures 2 and 3 (based on column "V excl.", tables 2, 3 and 4) illustrate the temporal variations in the feeding habits of *Coregonus pidschian* and *peled* in Vojmsjön, characterized mainly by the increase in the consumption of *Entomostraca* and flying and emerging insects during the icefree season. Though varying seasonally in their feeding habits the whitefishes like other salmonids (cf. ROOS, quoted by NILSSON 1955, NILSSON 1955, 1957) display a sort of learning on certain food objects, when these reach some state that makes them more easily available than any other food occurring in the fauna at that time: a changeable food specialization. For example nearly 100 per cent of all chironomid-larvae eaten by pidschian in July 1954 consisted of one species, *Constempellina brevicosta* EDW. (cf. BRUNDIN 1948), though this organism was certainly not the most abundant — not even the most abundant chironomid-larva. As no two sympatric species populations display exactly the same tendency of learning — though of course two specimens of different species can temporarily do it — this is the fundament of the formation of food niches and may be valid also for other groups of animals.

Even though a certain yearly rythm in the seasonal variations could be discerned there are also considerable annual variations. The important difference between the samples from 1949—1951 and 1954—1955 — mainly characterized by a disappearance of the molluscs *Planorbis* and *Valvata* and of the *Ephemeroptera, Plecoptera* and *Sialis* larvae (cf. Diagram, Fig. 4) —

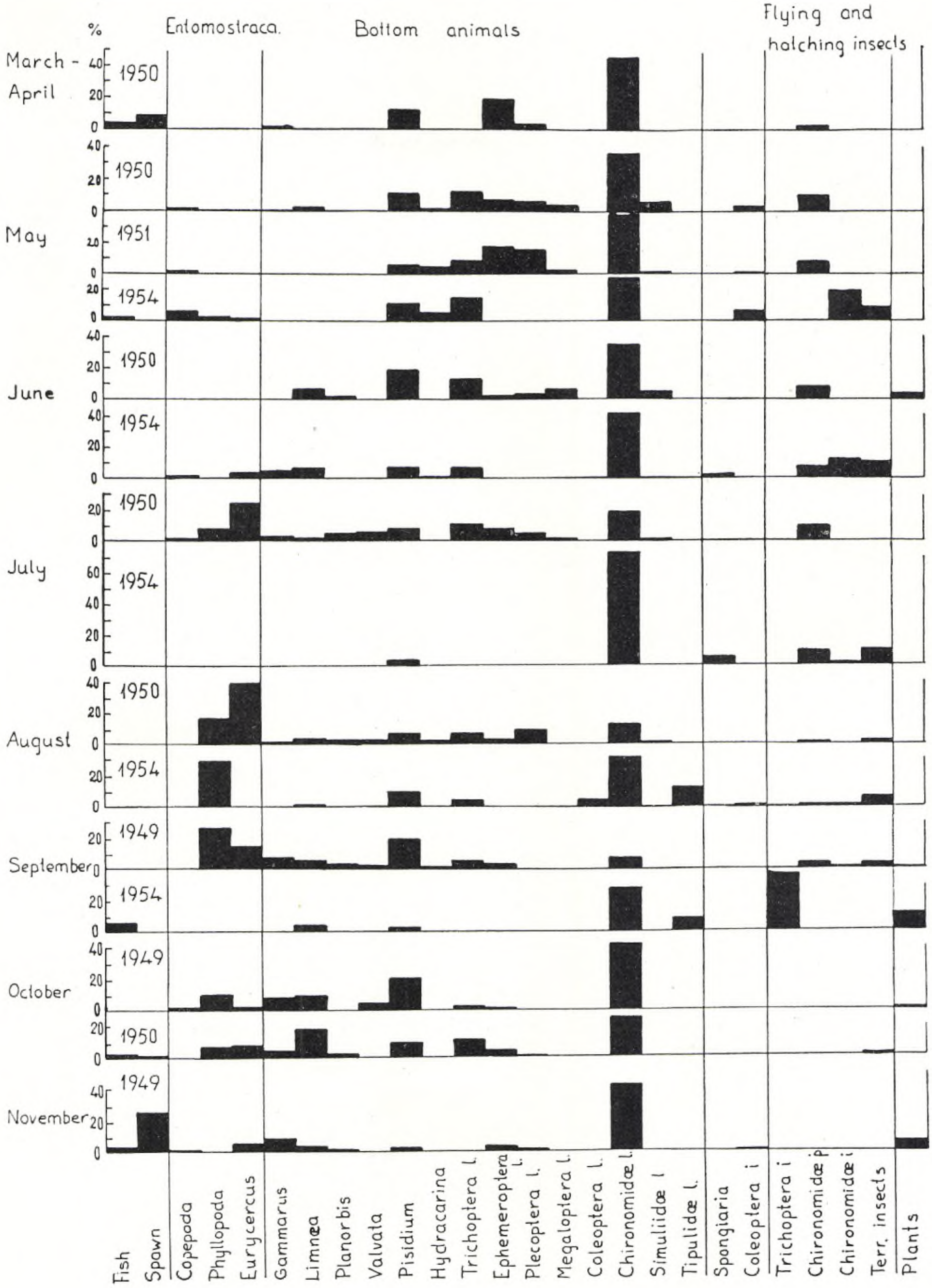

Fig. 2. The food of *Coregonus pidschian* in Lake Vojmsjön. Based on the column "V excl." in Tables 2. and 3.

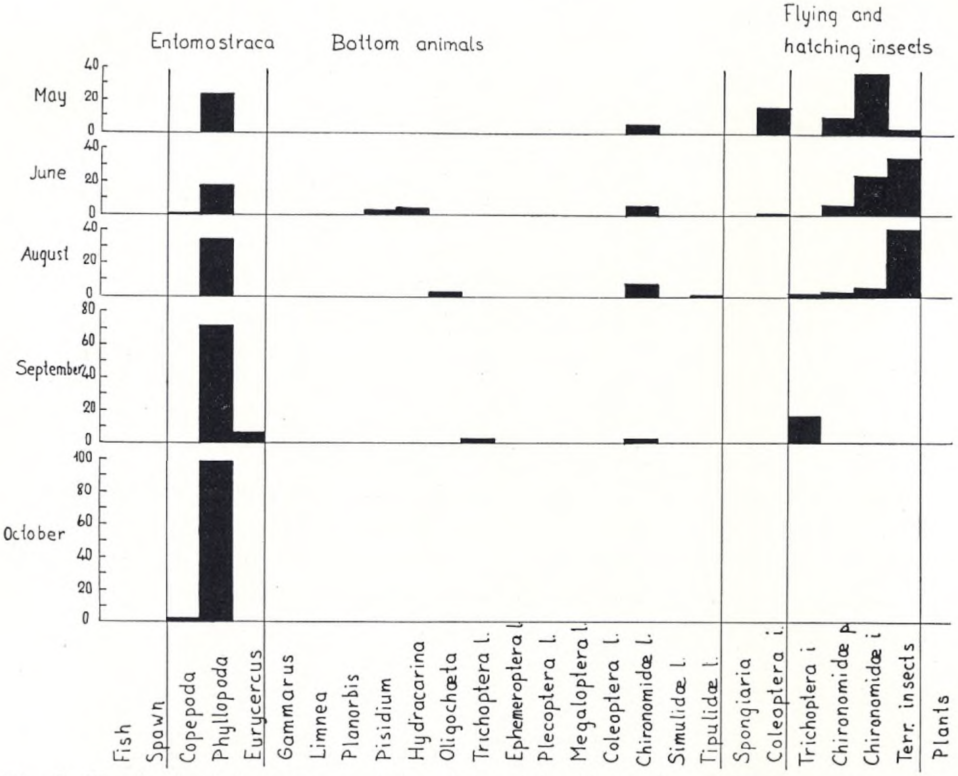

Fig. 3. The food of *Coregonus peled* in Lake Vojmsjön during 1954. Based on column "V excl." in Table 4.

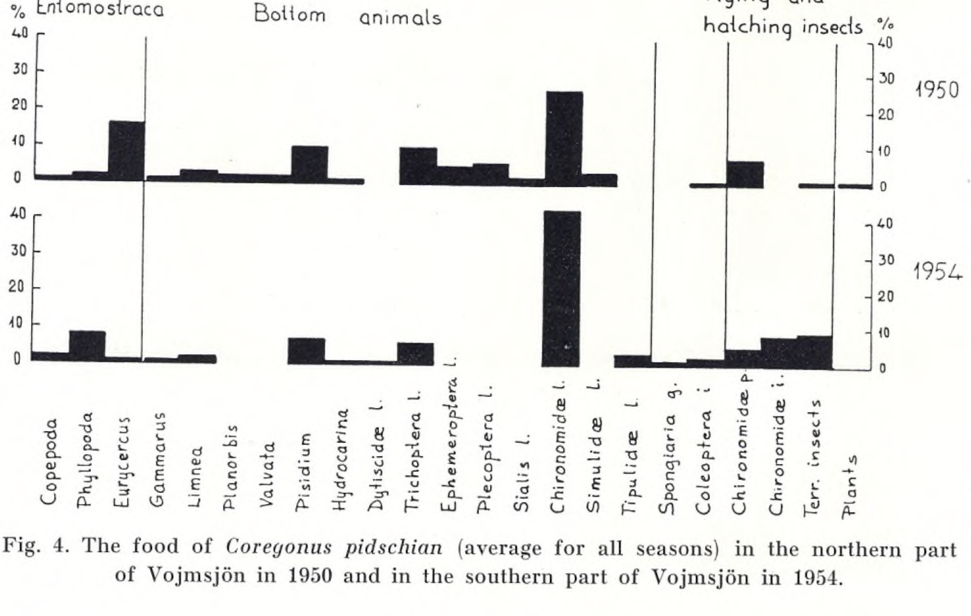

Fig. 4. The food of *Coregonus pidschian* (average for all seasons) in the northern part of Vojmsjön in 1950 and in the southern part of Vojmsjön in 1954.

certainly is the result of an altering and impoverishing effect of the regulation of the water-level (cf. DAHL 1926, 1932, HUITFELDT-KAAS 1935, RUNNSTRÖM 1946, NILSSON 1955, STUBE 1958).

3. Food competition between Coregonus pidschian and peled

On comparing the food of the two species during 1954 and 1955 (Diagrams, Figs. 2, 3, and 5) we immediately note the significant difference implying primarily that *pidschian* had fed mainly on bottom animals such as different species of molluscs, *Trichoptera, Chironomidae,* and other insect-larvae, *peled* mainly on crustacean plankton (mostly *Bosmina*). Moreover *pidschian* alone had consumed fish, *Gammarus,* sponges (*gemmulae*) and plants (mostly *Nostoc*), but *peled* to a greater extent than *pidschian Oligochaeta* and imagines of *Dytiscidae.* The insect-pupae and -imagines seem on the whole to have been shared by the two species, but this food did not always predominate in both species at the same time (cf. e.g. *peled*'s extensive consumption of terrestrial insects in August 1954, which had only a very

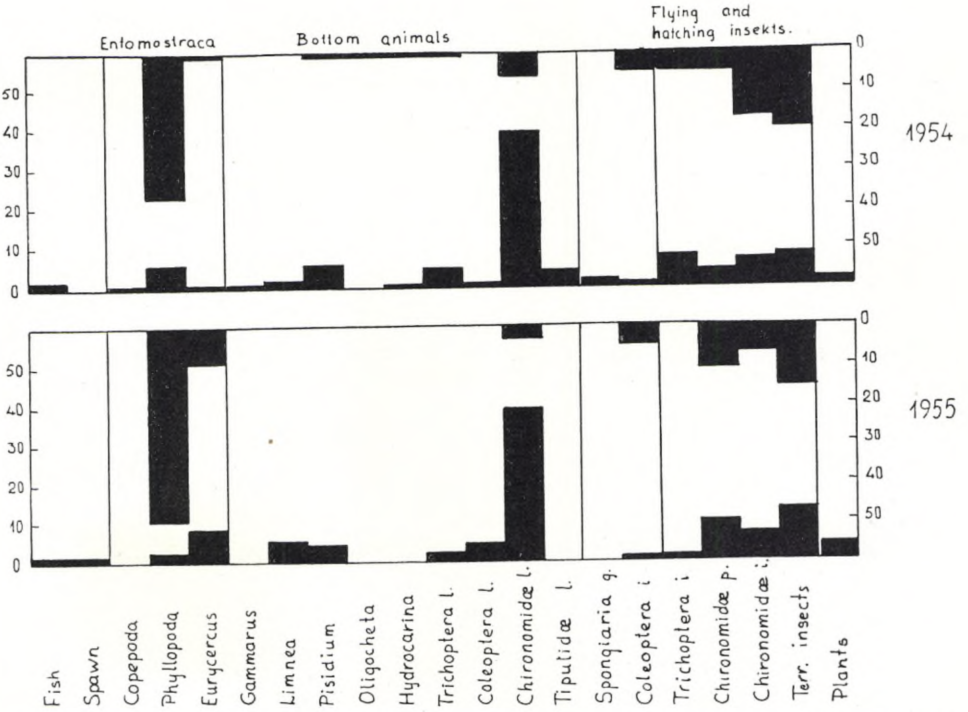

Fig. 5. The food of *Coregonus peled* (upper) and *pidschian* (lower) in 1954 and 1955 (average for all seasons).

weak parallel in *pidschian*. In a similar way the consumption of crustacean plankton did not culminate in both species at the same time: *pidschian* in August, *peled* in September—October (cf. also LINDSTRÖM 1955).

The present investigation confirms that LILLJEBORG's statement referred above is valid for two species living together in Vojmsjön. It is, however, also shown that this is no simple relationship: the food varies seasonally and annually, and there are such deviations within the species that the significant tendencies can only be discerned by taking into consideration a very great number of specimens. But why do not the *Coregonus*-species with dense gillrakers always eat plankton? To get a reasonable answer we may return to SVÄRDSON's (1954 a) theory. According to this theory with which the present author agrees the difference in growth rate is a result of the interspecific competition. It originates in a tendency of the consumption of food particles of different size which is realized by the pressure of competition, and which implies an isolating mechanism keeping the species in different ecological niches (cf. also SVÄRDSON 1954 b, 1958 a, b, NILSSON 1955, PEJLER 1957). When the species are living allopatrically without competition from closely related species there is consequently no corresponding pressure, which has as a result that *Coregonus*-species characterized in one lake by plankton-feeding and small size can under other conditions — e.g. when being transplanted into lakes with no original *Coregonus*-population (cf. SVÄRDSON 1950) — consume food objects optimal to the individual fish (cf. NILSSON 1955, 1956), and grow up to big sizes.

One question, however, raises itself immediately: in what degree are the differences due to the difference in average size, in what degree to inherent preferences to certain food objects?

In table 1 the fish caught in August and September 1954 have been distributed into three size groups, and their dominating food has been calculated as percentage of fish examined.

It can be seen from the table that in both species small food objects, such as *Bosmina,* had been eaten mainly by the smallest fish. The size of the fish is thus to a certain degree decisive for the choice of food, but the tendency to prefer plankton is much more marked in *peled* than in *pidschian,* 82 per cent of the *peled*-specimen less than 150 mm in length having eaten *Bosmina,* but only 47 per cent of the *pidschian*-specimen of the same length, 35 per cent of the *peled*-specimen between 150—250 mm in length, but no *pidschian*-specimen of that size. For other food items the difference appears to be still more important, independent of which size-group the fish belonged to.

On the whole the present material supports the idea that there exist between the two species inherent differences in their preference of food objects or habitats where different food organisms occur, but these are best noticeable, when the species compete with each other. The problem of the rôle of

Table 1. The dominating food of whitefish of three different sizes calculated as percentage of fish examined.

Size grop	<150		150—249		>250	
	Peled	Pidschian	Peled	Pidschian	Peled	Pidschian
Fish		6				
Bosmina	82	47	35			
Eurycercus			7			
Pisidium				10		20
Trichoptera l.		6	3			
Chironomidae l.	6	17	3	43		20
Tipulidae l.		12		14		
Oligochaeta			4			
Trichoptera i.	6		10	28	33	40
Chironomidae p.			3			
Chironomidae i.			4			
Terr. insects	6		31		67	20
Plants		12		5		

the gillrakers is still unsolved, but LILLJEBORG's statement — if interpreted in a wide sense — holds good, as there is a correlation on one hand between the number of gillrakers and the growth rate, on the other hand between the feeding habits and the growth rate.

4. Summary

1. The problem of the correlation between the number of gillrakers, the growth rate and the feeding habits of whitefish was studied on 1,126 *Coregonus pidschian* and 430 *Coregonus peled* from Lake Vojmsjön in southern Swedish Lapland.

2. The feeding habits of the two species were found to vary with the size of the fish as well as seasonally and anually. It is suggested that a changeable food specialization, as is wellknown in salmonid fishes, is the fundament of the formation of food niches and may be valid also for other groups of animals. A regulation of the water-level is supposed to have altered and impoverished the prey fauna of the lake.

3. Important differences were found in the feeding habits of the two species. The smaller species with numerous gillrakers (*C. peled*) had fed mainly on *Entomostraca*. The differences could be discerned also, if the fish were distributed into size-groups.

4. The present findings support SVÄRDSON's theory (1954) that the differences in growth rate between sympatric species of *Coregonus* are results of interspecific competition, implying a preference for food objects of different size, which affects the growth rate and the keeping of the species in different ecological niches.

Table 2. The food of *Coregonus pidschian* during 1949, 1950 and 1951.

	1949												1950							
	September				October				November				March—April				May			
Number of specimen	85				83				47				36				83			
Method	V excl.	V incl.	F	D	V excl.	V incl.	F	D	V excl.	V incl.	F	D	V excl.	V incl.	F	D	V excl.	V incl.	F	D
Fish									3.4	2.0	2.0	2.0	4.0	2.8	2.8	2.8				
Spawn									24.7	14.7	19.1	17.0	9.2	6.4	11.1	8.2				
Copepoda	0.1	0.1	2.4	—	1.5	1.0	6.0	—	0.5	0.3	4.3	—					0.9	0.8	3.6	1.2
Phyllopoda, plankt...	26.3	18.8	28.2	21.2	10.3	6.8	18.1	8.4												
Eurycercus	13.9	10.0	15.3	10.6	1.5	1.0	3.6	1.2	5.4	3.2	10.6	4.3								
Ostracoda																	0.1	0.1	1.2	—
Gammarus	7.0	5.0	11.8	5.9	7.7	5.1	14.5	4.8	7.7	4.6	10.6	6.4	2.4	1.7	5.6	2.8				
Limnaea	4.6	3.3	8.2	3.5	8.7	5.8	12.0	6.0	2.7	1.6	4.3	2.0					2.3	2.0	4.8	3.6
Valvata	1.5	1.1	4.7	—	4.1	2.7	3.6	3.6	0.2	0.1	2.0	—					0.1	0.1	1.2	—
Planorbis	3.3	2.4	8.2	2.4					0.7	0.4	2.0	—					0.1	0.1	2.4	—
Pisidium	19.3	13.8	32.9	12.9	19.8	13.1	38.6	10.8	1.7	1.0	8.5	—	12.5	8.7	25.0	5.6	10.5	9.1	30.1	10.8
Hydracarina	1.1	0.8	8.2	—	0.1	0.1	2.4	—	<0.1	<0.1	2.0	—					0.6	0.5	3.6	—
Trichoptera l.	4.6	3.3	4.7	3.5	1.8	1.2	8.4	—	0.2	0.1	6.4	—					11.6	10.1	15.7	12.0
Ephemeroptera l.	2.9	2.1	3.5	1.2	0.9	0.6	8.4	—	3.4	2.0	14.9	2.0	19.5	13.5	16.7	13.9	7.4	6.4	18.1	6.0
Plecoptera l.	0.1	0.1	3.5	—					0.8	0.5	2.0	—	4.0	2.8	2.8	2.8	6.0	5.2	15.7	4.8
Megaloptera l. (Sialis)					0.1	0.1	2.4	—	0.2	0.1	2.0	—					4.0	3.5	10.8	3.6
Chironomidae l.	7.1	5.1	30.6	3.5	42.1	27.9	50.6	31.3	41.9	25.0	42.6	23.4	46.5	32.2	52.8	33.3	36.7	31.8	69.9	31.3
Simulidae l.																	5.9	5.1	16.9	4.8
Coleoptera i. (Dytiscidae)					<0.1	<0.1	1.2	—	0.5	0.3	2.0	—					2.9	2.5	7.2	2.4
Chironomidae p.	3.6	2.6	11.8	2.4									1.9	1.3	2.8	—	10.3	8.9	21.7	6.0
Chironomidae i.	0.6	0.4	1.2	—																
Terr. insects	3.3	2.4	7.1	3.5													0.9	0.5	2.4	—
Plants	0.7	0.5	4.7	1.2	1.4	0.9	10.8	—	6.2	3.7	4.3	2.0								
Empty		28.2	28.2	28.2		33.7	33.7	33.7		40.4	40.4	40.4		30.6	30.6	30.6		13.3	13.3	13.3

Tab. 2 (continued).

	1950																1951			
	June				July				August				October				May			
Number of specimen	39				43				88				71				75			
Method	V excl.	V incl.	F	D	V excl.	V incl.	F	D	V excl.	V incl.	F	D	V excl.	V incl.	F	D	V excl.	V incl.	F	D
Fish													2.9	2.0	2.8	1.4				
Spawn													2.0	1.4	2.8	1.4				
Copepoda					1.3	1.2	4.7	—	0.3	0.3	1.1	—	0.5	0.4	2.8	—	1.3	1.1	8.0	—
Phyllopoda, plankt...					6.6	6.3	20.9	2.3	16.0	14.5	22.7	18.2	7.0	4.8	5.6	5.6				
Eurycercus					23.8	22.7	41.9	27.9	39.4	35.7	47.7	44.3	8.3	5.7	14.1	7.0				
Ostracoda													1.7	1.2	1.4	1.4				
Gammarus					1.7	1.6	4.7	2.3	0.7	0.6	1.1	1.1	3.7	2.6	9.9	2.8	0.1	0.1	2.7	—
Limnaea	5.9	5.6	15.4	7.7	0.9	0.9	4.7	—	2.9	2.6	15.9	1.1	18.2	12.4	22.5	12.7				
Valvata					5.0	4.8	7.0	7.0	2.2	2.0	2.3	2.3								
Planorbis	1.2	1.1	2.6	—	3.7	3.5	16.3	—	1.8	1.6	3.4	2.3	2.0	1.4	1.4	1.4				
Pisidium	18.0	17.0	48.7	15.4	6.6	6.3	27.9	7.0	5.5	5.0	26.1	3.4	8.6	5.9	16.9	5.6	4.7	4.1	18.7	2.7
Hydracarina					<0.1	<0.1	4.7	—	0.6	0.5	6.8	—					4.4	3.8	10.7	2.7
Trichoptera l.	12.4	11.7	20.5	12.8	10.0	9.5	14.0	14.0	5.5	4.9	6.8	5.7	10.6	7.2	11.3	8.5	7.6	6.6	9.3	8.0
Ephemeroptera l. ...	1.7	1.6	7.7	—	6.5	6.2	20.9	4.7	2.1	1.9	14.8	1.1	4.0	2.7	7.0	2.8	17.1	14.8	34.7	18.7
Plecoptera l.	3.0	2.8	15.4	2.6	4.3	4.1	18.6	7.0	8.2	7.4	22.7	4.5	1.1	0.8	4.2	—	14.9	12.9	33.3	13.3
Megaloptera l. (Sialis)	6.0	5.6	12.8	7.7	1.3	1.2	4.7	2.3									2.1	1.8	8.0	—
Chironomidae l.	34.6	32.7	82.1	30.8	17.8	17.0	69.8	16.3	12.3	11.1	48.9	4.5	25.0	16.9	36.6	15.6	38.1	33.0	69.3	36.0
Simulidae l.	5.2	4.9	12.8	2.6	1.0	1.0	4.7	—	0.7	0.6	2.3	—					0.5	0.4	4.0	—
Coleoptera i. (Dytiscidae)					<0.1	<0.1	2.3	—									1.0	0.9	4.0	—
Chironomidae p.	7.6	7.2	25.6	10.3	9.4	9.0	41.0	4.7	0.7	0.6	2.3	1.1					7.7	6.7	17.3	5.3
Chironomidae i.																				
Terr. insects	0.1	0.1	2.6	—	<0.1	<0.1	2.3	—	1.8	1.6	4.5	1.1	2.0	1.4	1.4	1.4	0.5	0.4	1.3	—
Plants	4.3	4.1	10.3	5.1					<0.1	<0.1	1.1	—	1.1	0.8	4.2	—				
Empty		5.1	5.1	5.1		4.7	4.7	4.7		9.1	9.1	9.1		32.4	32.4	32.4		13.3	13.3	13.3

V = Mean volumetrical percentage
F = Frequency
D = Dominating food object
excl. = empty stomachs excluded
incl. = „ „ included

Table 3. The food of *Coregonus pidschian* during 1954 and 1955.

	1954																			
	May				June				July				August				September			
Number of specimen	143				90				26				32				30			
Method	V excl.	V incl.	F	D	V excl.	V incl.	F	D	V excl.	V incl.	F	D	V excl.	V incl.	F	D	V excl.	V incl.	F	D
Fish	1.7	0.7	0.7	0.7													6.4	4.3	6.7	3.3
Spawn																				
Copepoda	5.0	2.1	2.8	2.8	0.9	0.8	1.1	1.1												
Phyllopoda	1.7	0.7	1.4	0.7									28.6	20.5	25.0	25.0				
Eurycercus	1.2	0.5	1.4	0.7	2.8	2.3	3.3	3.3					0.3	0.2	4.3	—				
Gammarus					4.4	3.6	5.6	4.4												
Limnaea	0.2	0.1	0.7	—	5.7	4.7	8.9	5.6					0.7	0.5	4.3	—	4.2	2.8	13.3	—
Pisidium	9.5	4.0	14.7	4.1	5.7	4.4	13.3	1.1	2.7	2.3	15.4	—	9.3	6.7	12.5	6.3	3.0	2.0	6.7	3.3
Oligochaeta													0.7	0.5	6.3	—	1.5	1.0	3.3	—
Hydracarina	3.6	1.5	2.1	1.4	1.8	1.5	2.2	1.1												
Trichoptera l.	14.3	6.0	7.0	6.3	6.0	4.9	7.8	4.4					4.3	3.1	6.3	4.3				
Coleoptera l.													3.8	2.7	15.6	—				
Chironomidae l.	26.8	11.2	20.3	11.2	41.0	33.7	46.7	36.8	72.2	61.0	76.9	65.5	31.2	22.5	31.3	25.0	27.7	18.5	30.0	16.7
Tipulidae l.	<0.1	<0.1	0.7	—	0.1	0.1	1.1	—					12.4	8.9	12.5	9.4	7.8	5.2	10.0	6.7
Spongiaria (gemmulae)					0.6	0.6	1.1	1.1	4.5	3.8	3.8	3.8								
Notonecta i.																				
Coleoptera i. (Dytiscidae)	5.7	2.4	4.1	2.8	0.3	0.3	2.2	—					0.8	0.6	4.3	—				
Trichoptera i.					0.1	0.1	1.1	—									37.3	24.8	26.7	26.7
Chironomidae p.	0.7	0.3	3.5	—	7.2	5.9	8.9	4.4	9.3	7.9	23.1	3.8	0.8	0.6	6.3	—				
Chironomidae i.	19.3	8.1	5.6	3.5	12.0	9.9	16.7	10.0	1.5	1.3	7.7	—	0.8	0.6	6.3	—				
Terr. insects	9.0	3.8	8.4	4.1	11.4	9.4	15.6	8.9	9.8	8.3	15.4	11.5	6.3	4.5	12.5	4.3	1.2	0.8	3.3	—
Plants																	10.9	7.3	10.0	10.0
Sand	1.2	0.5	2.1	0.7																
Empty		58.0	58.0	58.0		17.8	17.8	17.8		15.4	15.4	15.4		28.1	28.1	28.1		33.3	33.3	33.3

Tab. 3 (continued).

	1954									1955							
	October			November			December			May—June				September			
Number of specimen	11			14			13			73				44			
Method	V incl.	F	D	V incl.	F	D	V incl.	F	D	V excl.	V incl.	F	D	V excl.	V incl.	F	D
Fish										2.3	1.4	1.4	1.4				
Spawn										2.3	1.4	1.4	1.4				
Copepoda																	
Phyllopoda										2.9	1.8	2.7	2.7				
Eurycercus														15.5	6.0	10.0	6.6
Gammarus																	
Limnaea	5.5	9.0	9.0							3.6	2.2	4.1	2.7	6.0	2.3	4.5	2.2
Pisidium	6.3	27.3	—				2.3	7.7	—	5.5	3.4	11.0	1.4	2.3	0.9	4.5	—
Oligochaeta																	
Hydracarina																	
Trichoptera l.														3.6	1.4	2.2	2.2
Coleoptera l.										2.3	1.4	2.7	2.7	5.2	2.0	2.2	2.2
Chironomidae l.	5.5	27.3	—	7.0	7.0	7.0				35.4	21.9	31.5	23.3	42.6	16.4	22.7	15.6
Tipulidae l.																	
Spongiaria (gemmulae)										0.6	0.4	1.4	—				
Notonecta i.										0.2	0.1	1.4	–	0.8	0.3	2.2	—
Coleoptera i. (Dytiscidae)																	
Trichoptera i.														2.3	0.9	2.2	—
Chironomidae p.										19.8	12.2	20.5	11.0	0.5	0.2	2.2	—
Chironomidae i.										13.1	8.1	16.4	8.2				
Terr. insects										4.2	2.6	8.2	1.4	21.2	8.2	10.0	9.8
Plants	37.2	45.5	45.5				5.4	7.7	7.7	7.8	4.8	5.5	5.5				
Sand																	
Empty	45.5	45.5	45.5	93.0	93.0	93.0	92.3	92.3	92.3		38.4	38.4	38.4		61.4	61.4	61.4

V = Mean volumetrical percentage
F = Frequency
D = Dominating food object
excl. = empty stomachs excluded
incl. = ,, ,, included

Table 4. The food of *Coregonus peled* during 1954 and 1955.

	1954																	
	May				June				August			September				October		
Number of specimen	32				46				31			55				59		
Method	V excl.	V incl.	F	D	V excl.	V incl.	F	D	V incl.	F	D	V excl.	V incl.	F	D	V incl.	F	D
Copepoda					0.9	0.7	2.2	—								1.0	1.7	1.7
Phyllopoda	24.1	8.3	12.5	9.4	17.6	13.0	13.0	13.0	35.0	38.7	38.7	72.2	47.4	47.4	47.4	49.7	50.8	49.2
Eurycercus												5.5	3.6	3.6	3.6			
Limnaea					0.3	0.2	2.2	—										
Pisidium					2.9	2.2	2.2	2.2	0.2	3.2	—							
Oligochaeta									3.1	3.2	3.2							
Hydracarina					3.5	2.6	4.3	2.2										
Trichoptera l.												2.8	1.8	1.8	1.8			
Coleoptera l.									0.3	6.4								
Chironomidae l.	5.5	1.9	15.6		5.6	4.1	10.9	6.5	7.9	16.1	6.4	2.8	1.8	1.8	1.8	0.1	1.7	—
Tipulidae l.									1.0	3.2	—							
Dixidae l.									0.6	3.2	—							
Coleoptera i.	17.3	5.9	9.4	6.3	1.2	0.9	2.2	—										
Trichoptera i.									1.8	3.2	3.2	16.7	10.9	10.9	10.9			
Chironomidae p.	10.9	3.8	6.3	3.1	7.1	5.2	8.7	4.3	2.9	6.4	3.2							
Chironomidae i.	38.2	13.1	18.8	15.6	25.0	18.5	32.6	17.4	5.5	9.7	3.2							
Terr. insects	3.5	1.3	3.1		35.9	26.5	37.0	28.3	41.8	54.8	41.9							
Sand	0.5	0.2	3.1															
Empty		65.5	65.5	65.5		26.1	26.1	26.1	00.0	00.0	00.0		34.5	34.5	34.5	49.2	49.2	49.2

Tab. 4 (continued).

	1954						1955							
	November			December			May—June				September			
Number of specimen	47			37			70				53			
Method	V incl.	F	D	V incl.	F	D	V excl.	V incl.	F	D	V excl.	V incl.	F	D
Copepoda	10.2	10.6	10.7								0.7	0.5	5.7	—
Phyllopoda	14.9	14.9	14.9				61.3	20.2	21.4	20.2	38.6	25.5	28.3	28.3
Eurycercus											17.7	9.7	13.2	9.4
Limnaea											0.1	0.1	1.9	—
Pisidium											0.1	0.1	1.9	—
Oligochaeta														
Hydracarina														
Trichoptera l.														
Coleoptera l.														
Chironomidae l.	2.6	4.3	2.1				1.5	0.5	2.9	—	3.6	2.4	11.3	1.8
Tipulidae l.														
Dixidae l.														
Coleoptera i.				2.7	2.7	2.7					9.4	6.2	15.1	5.7
Trichoptera i.											0.6	0.3	1.9	—
Chironomidae p.							21.5	7.1	10.0	8.6	0.9	0.5	3.8	—
Chironomidae i.							8.3	2.7	5.7	1.4	6.3	4.2	11.3	3.8
Terr. insects							7.4	2.4	2.9	2.9	25.0	16.5	22.6	17.0
Sand														
Empty	72.3	72.3	72.3	97.3	97.3	97.3		67.1	67.1	67.1		34.0	34.0	34.0

V = Mean volumetrical percentage
F = Frequency
D = Dominating food object
excl. = empty stomachs excluded
incl. = „ „ included

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The Fauna of a Regulated Lake

By Maj Stube

Contents

I. Introduction

In the north-western part of Jämtland at Lat. 64°06′ N. towards the boundary against Västerbotten Lake Borgasjön, belonging to the drainage system of Ångermanälven, is situated Fig. 1. It covers a surface of 11.4 sq.kms., and is surrounded by mixed forests of birch and conifers. The height above sea-level is 450.8 ms. In connection with our supply of electric energy one of the most extensive regulations of lakes of later times in Sweden has been carried out here, the amplitude of the regulation being 18 metres.

Since this damming-up was bound to constitute a far-reaching interference with the biological processes, an examination of the fauna was carried out in 1948 and 1949, prior to the regulation of the lake, and others in 1954 and

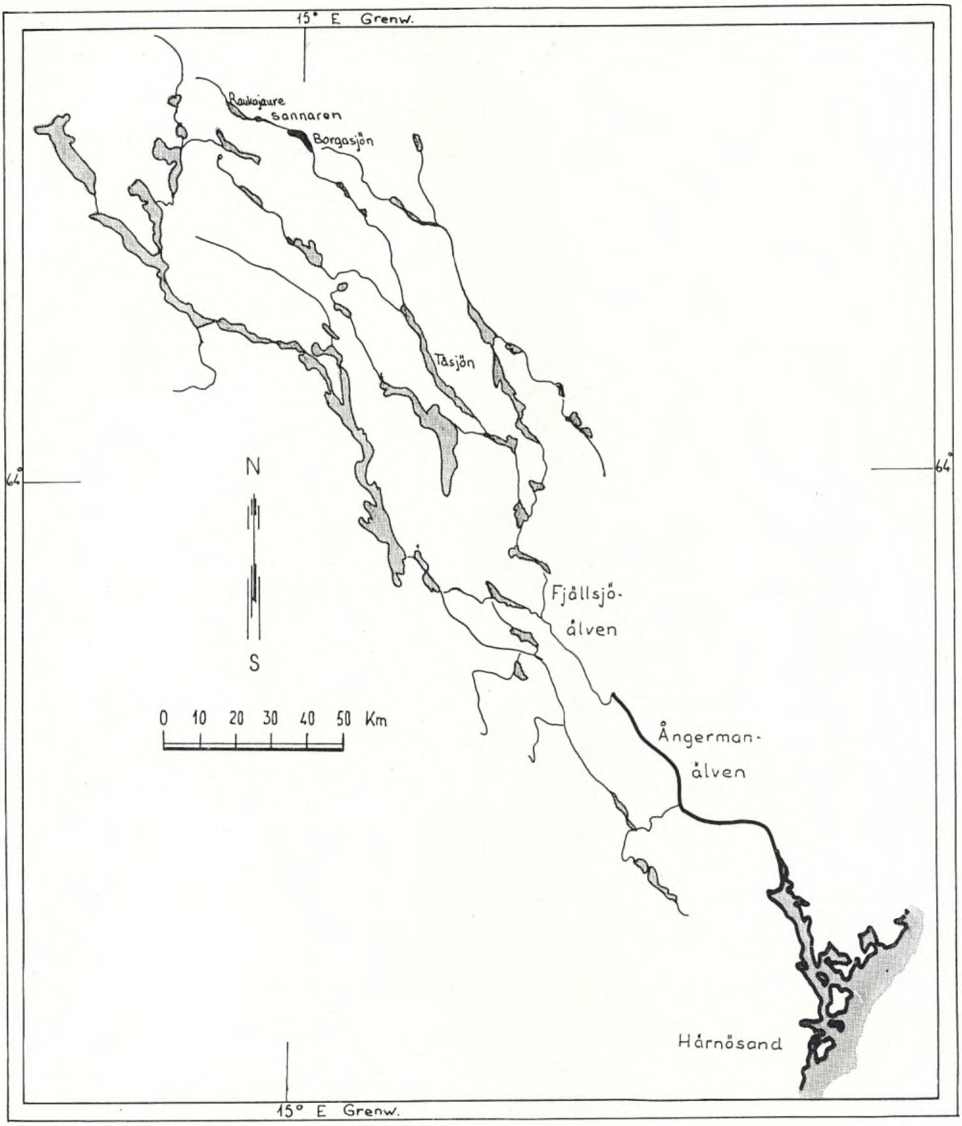

Fig. 1. The geographical situation of Lake Borgasjön and Lake Sannaren.

1957, when the lake had already for two and five years been under the influence of the regulation. The interest was centered on the epifauna before the regulation but bottom fauna and fish fauna was also studied.

Borgasjön belongs tothe oligotrophic type of lakes, and it was very difficult to find in the lake proper any rich vegetational belts suitable for epifauna studies.

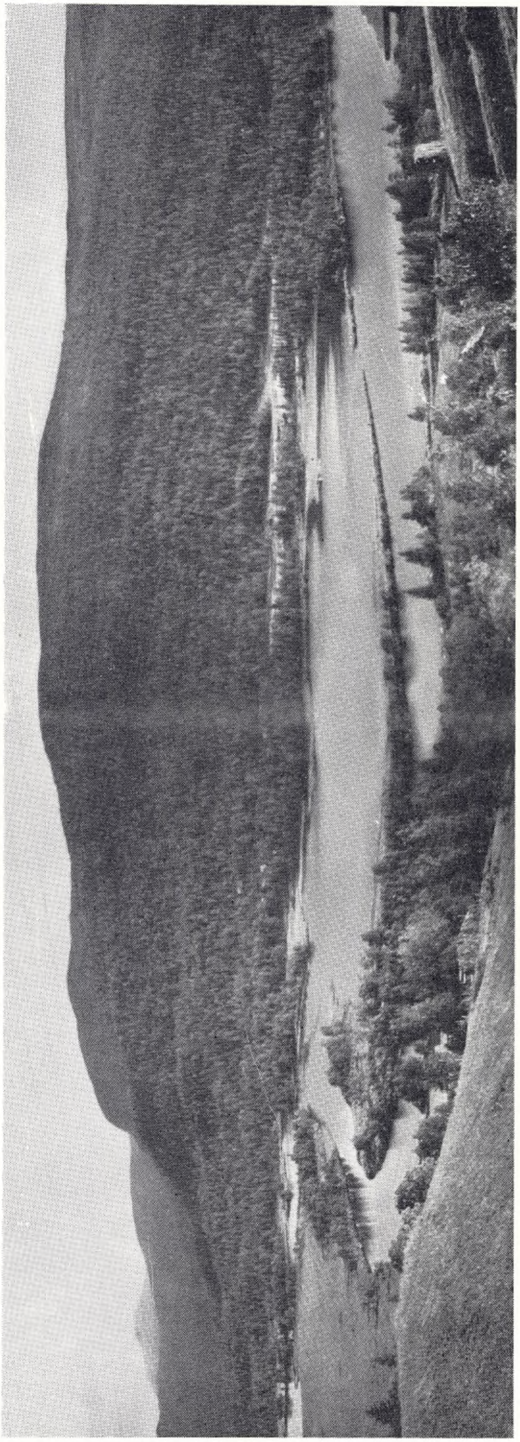

Fig. 2. The delta of River Sannarån in 1949 before regulation.

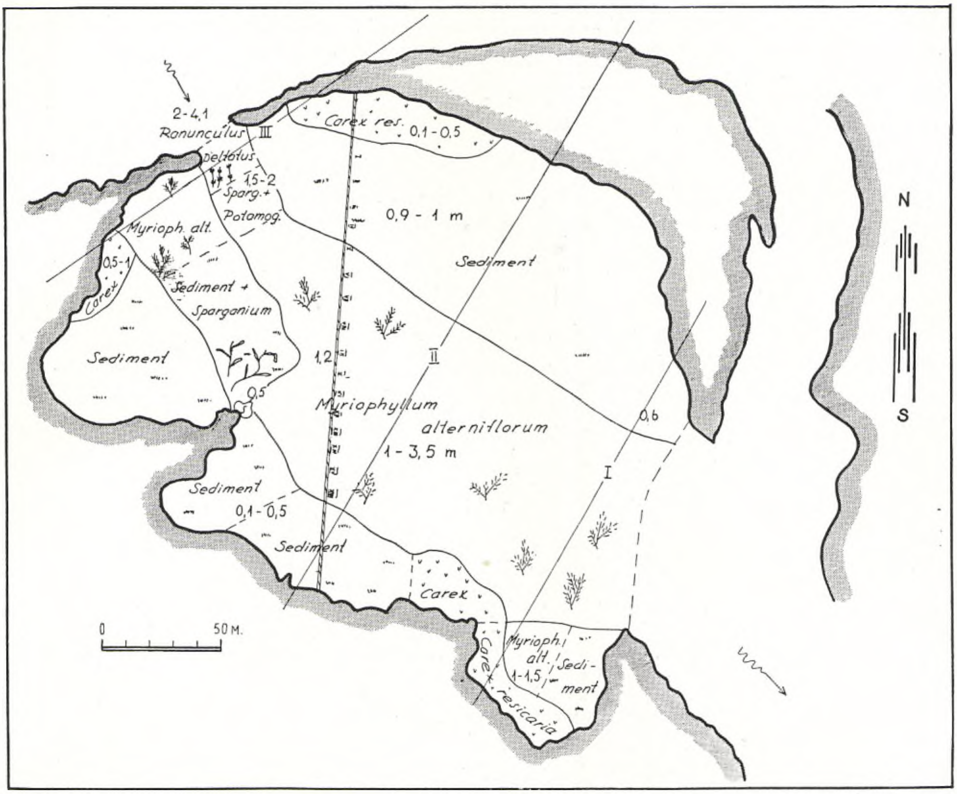

Fig. 3. Situation, size, and depth of the vegetational areas and the naked bottoms in the delta of River Sannarån. The thickest line represents the rope which after regulation was stretched across the former delta.

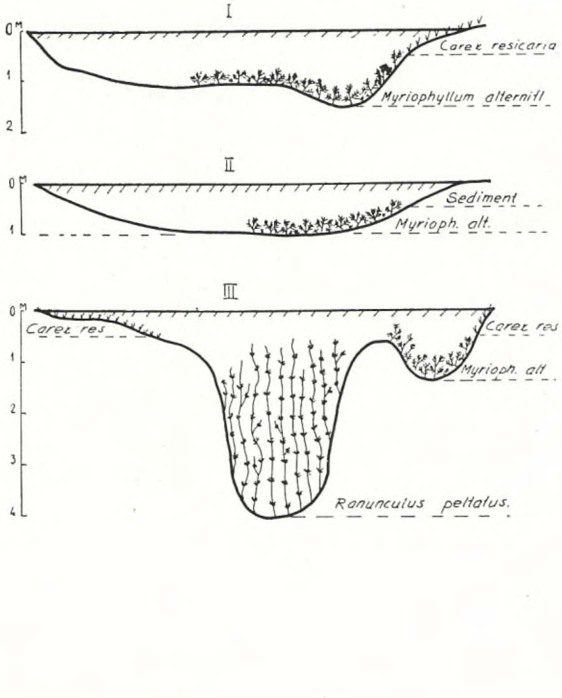

Fig. 4. Profiles of delta bottoms taken from the sections I—III, Fig. 3 in the delta of River Sannarån.

In the Sannarån, which discharges its water into the north-western end of Borgasjön three deltas, relatively rich in vegetation had been formed. The uppermost of these deltas (see Fig. 2) possessed an aquatic vegetation fit for sampling.

The vegetational regions contained *Carex vesicaria* at a depth of 0.1—0.5 m., *Myriophyllum alterniflorum* at 1—3.5 ms., *Ranunculus peltatus* at 2—4.1 ms, and *Sparganium sp.* and *Potamogeton gramineus* at the depth of 1.5—2.1 ms. Some isolated specimens of *Isoëtes* and *Hippurus vulgaris* have been found in some places. Situation, size, and depth of the vegetational areas can be seen from Figs. 3 and 4.

The examined area in the delta of the Sannarån occupied a surface of 43,730 sq.ms. Of these 42.5 per cent were formed by meadows of *Myriophyllum,* 48.7 per cent by naked sedimentary bottoms, i.e. bottoms free from macrophytes, 6.6 per cent, by belts of *Carex,* 1.3 per cent by mixed meadows of *Sparganium* and *Potamogeton,* 0.7 per cent by a vegetation of *Ranunculus,* and 0.2 by an area of very sparsely growing *Isoëtes.*

II. Material and Methods

In the vegetational and sedimentary soils about 900 samples, containing about 40,000 animals, have been taken.

1. Field procedure in sampling of plant fauna

Under normal conditions the ice on Borgasjön does not break up before the beginning of June. In 1949 spring and summer were cold. The collecting of the plant samples did not start before the end of June, as only then the plants had reached a stage of development which made netting possible. In every vegetational region a number of samples, spread over the entire period, were taken from the last two weaks of June to the end of August. A certain amount of withering could be noticed by the end of August and the beginning of September, indicating the termination of the growing season proper.

In the vegetational region the netting was carried out by means of a net with a handle and a sharp edge, the dimensions being shown in Fig. 5. Nearest to the iron it was shod with canvas, the bag of the net terminating in a straining-cloth of 0.4 mm. mesh. The net was carefully introduced into the vegetational belts so as not to touch the bottom. Whenever this nevertheless happened, the sample was discarded. Up to the depth of 4.1 ms., the greatest in the area, the bottom was clearly visible. The net could therefore be seen during work in all depths.

Each netted sample was transferred into a large bowl with water. The net was carefully rinsed above this bowl the contents of which were then passed

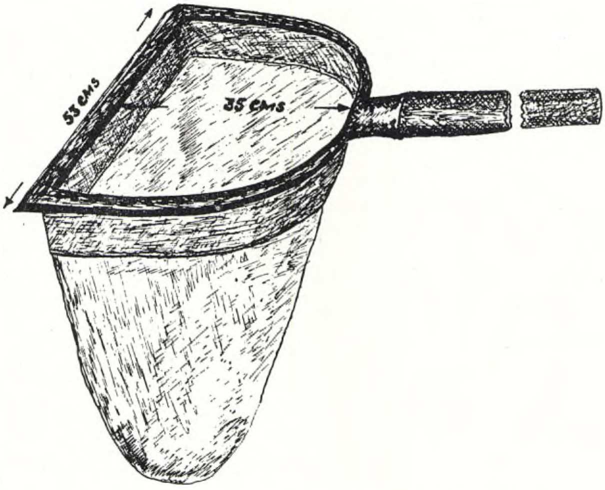

Fig. 5. The net for the macrophyte sampling.

through a sieve of brass wire gauze of 0.5 mm. mesh. Water from the place of the sampling was used in order to wash the epifauna off the plant sample. This was done in the bowl. The contents of the bowl were again passed through the sieve. At all these steps the water had previously been passed through a plankton net.

After washing, the plant sample was placed into absorbing paper until the shiny moist surface had disappeared. This took 3—5 minutes. The plant sample was subsequently weighed with a spring balance capable of adjustment. The remains in the sieve were preserved in a 5 % solution of formol.

In the belt of *Carex,* which had the shallowest position, the plants were carefully cut with a knife over the rim of the net. All parts of plants outside the net were excluded.

2. Field procedure in sampling of bottom fauna

In the taking of these samples a bottom grab according to EKMAN with an opening of 2.25 by 2.25 dms. was used. The contents were passed through the same sieve which is used for the plant samples. Before the regulation of the lake three samples were taken every month in the sedimentary region of every station (For situation and depth, see Fig. 3).

In the August of 1954, when the regulation of the lake had been in effect for two years, the sampling was carried out in a somewhat different way, since the bottoms had been re-deposited. A rope was stretched across the former delta (see Fig. 3), the rope being marked from ten to ten metres.

At every mark upon the rope ten samples were taken within the former delta. All samples from both examinations were preserved in a 5 % solution of formol.

3. Laboratory procedure for plant and bottom fauna samples

In the laboratory the field samples were sorted out with a binocular microscope, and transferred to 80 % alcohol in which they were allowed to remain at least two months before being examined. Students of this subject have made use of many different methods for the quantitative determination of the bottom fauna. If only the organic weight is determined, the weight method does not present any greater advantages over the volume method, the former being dependent upon many external factors. For the purposes of field work the volume method deserves preference over the weight method.

Every group of animals was examined separately in each sample, and the volume determined by placing the animals upon filter paper, where they remained until the disappearance of the moist sheen. They were then transferred into a test-tube of known volume, calibrated for 1 and 2 ccs. According to the size of the sample water was then added from a burette up to the 1 cc. or 2 ccs. mark. In the case of isolated small, not measurable animals the volume per individual, calculated from a sample with a greater number of individuals, was noted down together with the number of individuals in the sample in question.

According to Ball (1948) from whom the method is essentially derived there is "more variation between live weight and live volume than between live weight and preserved volume. For all groups of organisms considered, the conversion factor for changing preserved volume in cubic centimeters to an equivalent live weight in grams is 0.98". And therefore, he says, "for purposes of this study, 1 cc of preserved volume can be considered the same as 1 g. live weight".

4. Fish fauna: field and laboratory procedure

During the months of sampling of the year 1949 gill nets were placed in connection with the different vegetational belts. These nets were of different mesh, the finest having a stretched mesh of 1.76 cm., and the coarsest a stretched mesh of 8.56 cms. During the test fishing in the delta the upper and the lower opening of the delta were closed with nets in order to prevent as much as possible the entry of fish from the neighbourhood.

In the year 1950 a number of young brown trout in the delta of Sannarån had their fins cut, whereupon they were immediately liberated at the place of their capture.

In 1954 and 1957 renewed test fishing took place in the former delta and its vicinity.

The fish caught at the different occasions was immediately measured and weighed in the field, when also samples of scales and stomach were taken. The latter were numbered, wrapped up in gauze, and laid in 4 % formol. Care was taken to cut off the stomach at the pylorus. The contents of the stomach were preserved, and sorted in the same way as described above under 3 for the faunas of the plants and the bottom. The scale samples were prepared and read in a scale-reading apparatus by the personnel in the laboratory.

5. Reliability of the sampling methods

At present there exist no entirely reliable methods for the qualitative and quantitative determination of the epifauna or of the bottom animals.

In determining the fauna of the *Fucus* vegetation SEGERSTRÅLE (1927) has made use of the netting method. He has calculated the quantity of animals in grams for 1 kg. of *Fucus*.

MEUCHE (1939) carries out the quantitative determination of the epifauna according to an approximate scale with variation from rare (1—4), few (5—10), numerous, frequent, to innumerable animals. This method by estimation is too much dependent on the human factor.

ROSINE (1955) has carried out measurements of length on certain plants. The length of the stem was put into relation to surface and weight. From these figures he determined the surface of plant in sq.cms. per 10 cms. length of stem. A plant surface of 100 sq.cms. was considered the unit for the density of population of the animals.

The method used by BALL (1948) which has been applied in this investigation, ought to receive preference over the above-mentioned methods.

Many factors interfere, and cause errors. The random variation within a series of samples can be great. The type of weather varies between different years, and several scientists (BRUNDIN 1949, LENZ 1953, THIENEMANN 1954, and others) have shown this to influence also the density of the bottom animals in a lake. According to the same authors the variation is likewise determined by the seasons, as is borne out also by this investigation.

A criticism can of course be raised with regard to the choice of the mesh of the straining-cloth. ALM (1922) used wire gauze of 0.8—0.9 mm. mesh, OLSTAD (1925) 0.6 mm., VALLE (1927) 0.5—1.5 mm., LANG (1931) 0.6 mm., BERG (1938) 0.6 mm., and BRUNDIN (1949) 0.6 mm. A selection does of course take place. JÓNASSON (1955) has pointed out the great errors which arise especially in quantitative determinations of the bottom fauna from the different mesh of the straining-cloth. Perhaps a comparison factor for different types of straining-cloth will be gradually developed.

In the investigations in the delta of Sannarån the results have not been subjected to statistical treatment. For this reason a great number of equally distributed samples were taken within the area in order to make the sampling representative of the quantity of animals in the delta. As a check also occasional samples, "outside the program", were taken. The sampling was furthermore spread over the whole summer. This could to a certain extent counteract the selection of the straining-cloth, as the growth of certain animals made them gradually catchable.

All animals have been determined with the aid of suitable literature (see list of references). As every determination has been checked by the author in person, the number of determined animal species is not very large. A number of larvae can be determined specifically only by hatching.

III. Results

1. Epiphytes

Upon *Carex vesicaria* only some few epiphytes, like siliceous algae and green algae, were found.

Ranunculus peltatus (see Figs. 6 a and 6 b) carried a fair amount of epiphytes, especially at the spiny processes of the leaves. Among the epiphytes, present there, were

Chrysophyta: Achnanthes, Gomphonema, Tabellaria flocculosa, Eunotia pectinalis, Cymbella, and *Cocconeis*

Chlorophyta: Cosmarium, Zygnema, and *Pediastrum*

Cyanophyta: Merismopedia

Compared with the previously mentioned macrophytes *Myriophyllum* carried the greatest amount of epiphytes (see Figs. 7 a and 7 b). There occurred, in addition to those found upon *Ranunculus peltatus,* amongst others

Chlorophyta: Bulbochaëte and *Schizochlamys,* and among

Cyanophyta: Schizotrix

Fig. 6 a. *Ranunculus peltatus.* Submerged leaves with epiphytes.

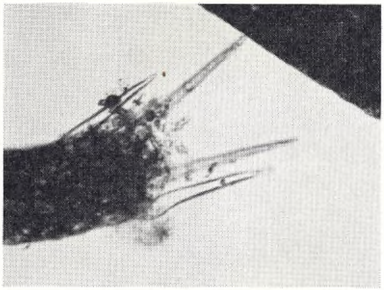

Fig. 6 b. *Ranunculus peltatus.* Detail of a leaf with the spiny processes.

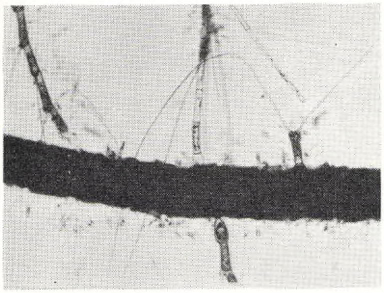

Fig. 7 a. *Myriophyllum alterniflorum.* Submerged leaf with epiphytes.

Fig. 7 b. *Myriophyllum alterniflorum.* Detail of a submerged leaf.

2. Epifauna

The distribution of the epifauna in the different vegetational zones during the three months of the investigations appears from the Figs. 8, 9, and 10, respectively. Comparisons are also made for every single group of animals. See Tables I, II, and III.

Oligochaeta. (Fig. 11)

In the samples from the delta of Sannarån the genera *Tubifex* and *Lumbriculus* were represented.

The tubificids, which have been found in the delta of Sannarån upon all examined plants, were most numerous upon *Myriophyllum* in July. This can only be explained by the fact that the vegetation of *Myriophyllum* contained an abundant admixture of mouldering leaves which were strongly covered with sediment. Upon the sedimentary bottoms, which — if rich in

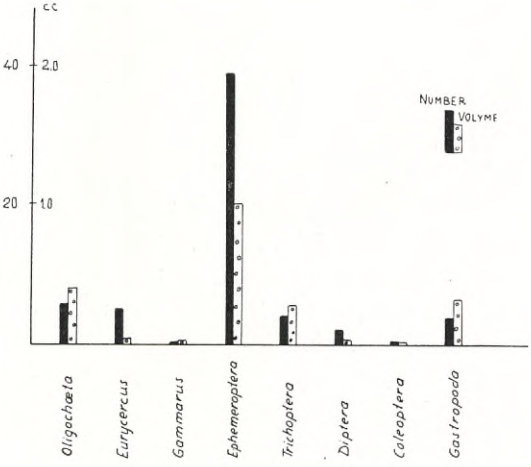

Fig. 8. Invertebrate fauna per kg. of *Carex vesicaria* collected by plant sampling in the delta of Sannarån in the summer 1949. Average number (left column), average volume (right column).

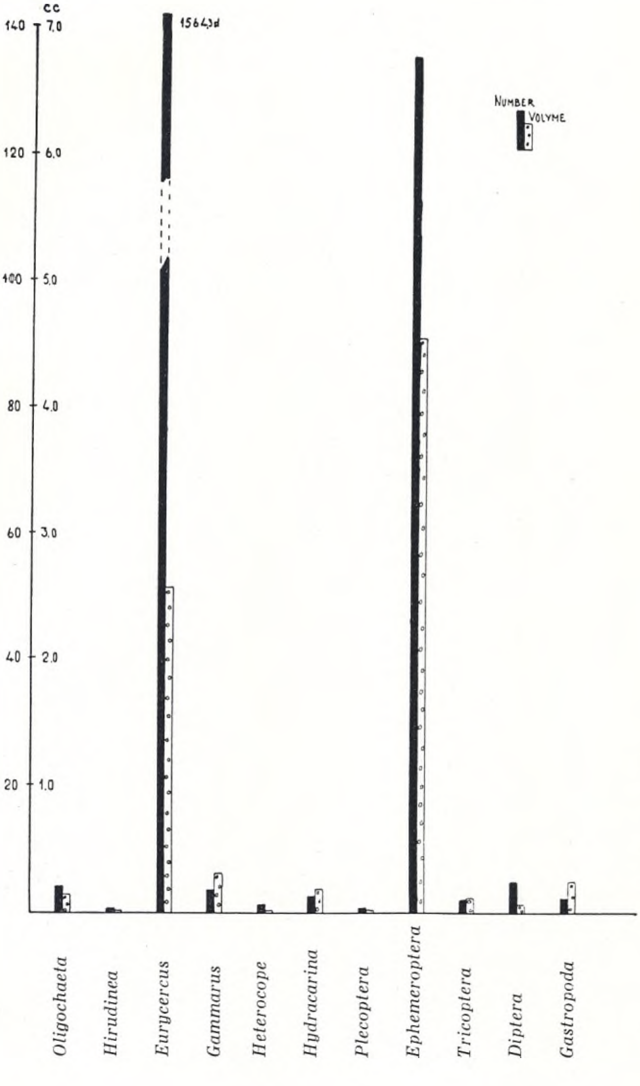

Fig. 9. Invertebrate fauna per kg. of *Ranunculus peltatus* collected by plant sampling in the delta of Sannarån in the summer 1949. (For symbols, see Fig. 8).

detritus — according to ALSTERBERG (1922) constitute their true biotope, *Tubifex sp.* occurred in much greater numbers. *Lumbriculus* was missing upon *Ranunculus peltatus,* but occurred upon the other plants. It lives in about the same biotope as Tubifex, but occurs according to VALLE (1927) more in the vegetational region. On account of the fact that *Lumbriculus* does not build tubes it is also more mobile. Compared with the other plants *Ranunculus peltatus* was freest from detritus, and this fact may explain the absence of *Lumbriculus.*

Hirudinea. (Fig. 12)

The investigation in the delta of Sannarån shows with full evidence that

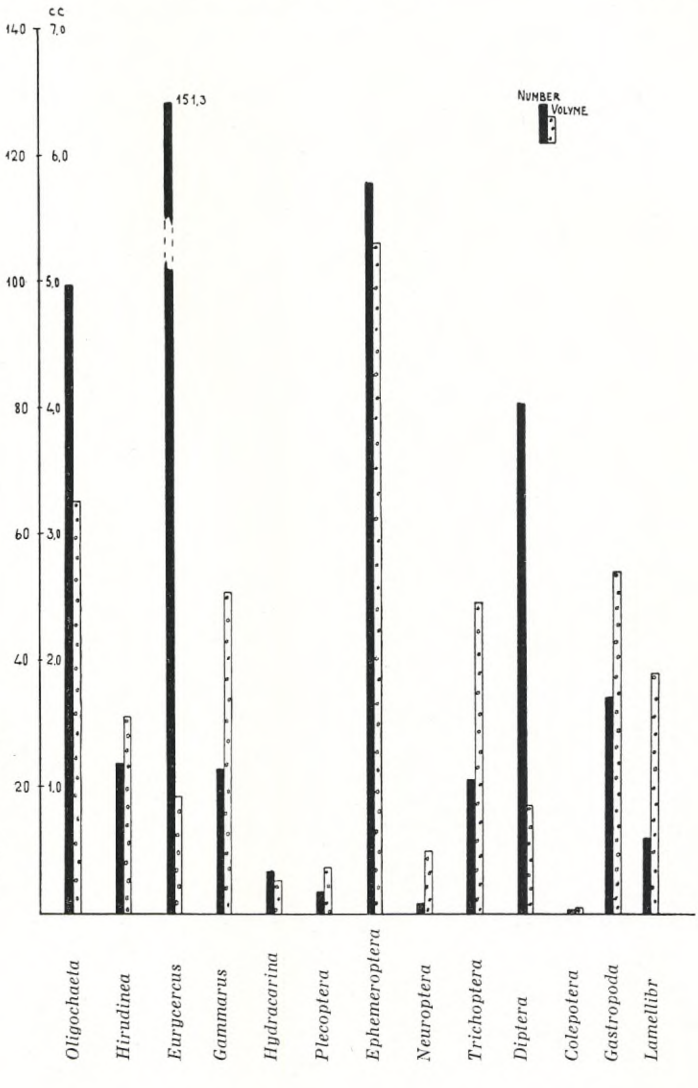

Fig. 10. Invertebrate fauna per kg. of *Myriophyllum alterniflorum* collected by plant sampling in the delta of Sannarån in the summer 1949. (For symbols, see Fig. 8).

the hirudineans (Fig. 12), in this case *Helobdella stagnalis,* like the oligochaetes prefer *Myriophyllum alterniflorum* to *Ranunculus peltatus* (Tables II and III). Here, however, the explanation seems to be another one. They prefer (BOISEN-BENNIKE 1943) biotopes which, apart from a good supply of food, afford suitable surfaces for fixation. Thus *Myriophyllum* with its dense growth ought to offer a better foothold than *Ranunculus peltatus,* while it at the same time supplies a greater amount of animals which are suitable as food for *Helobdella.*

The temperature (BOISEN-BENNIKE 1943) has proved to be a limiting factor, since no leeches have been found in running water the temperature of which has not been above 11°C for a longer period.

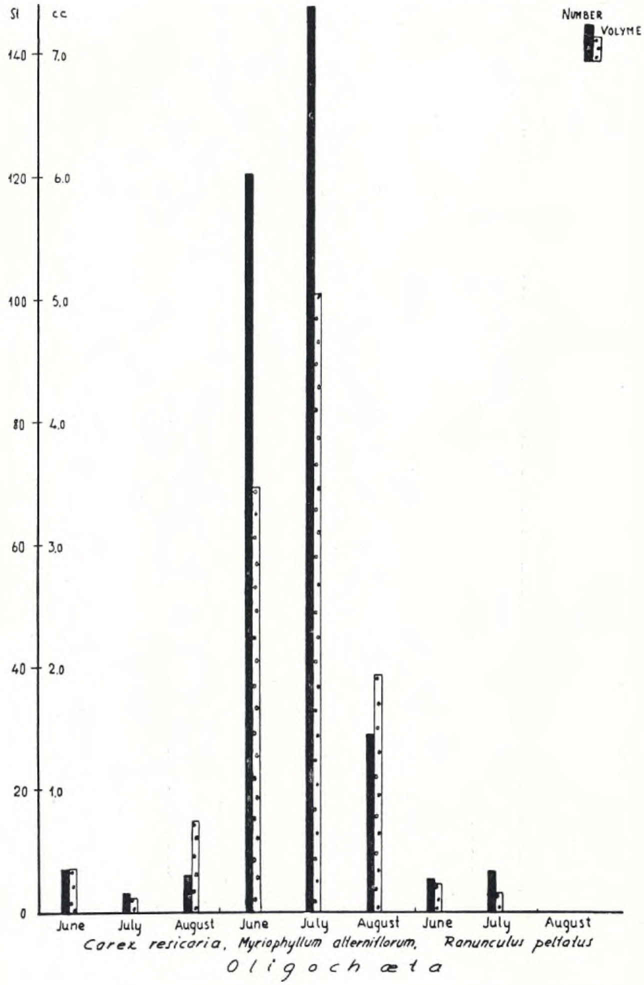

Fig. 11. Seasonal changes in the abundance of *Oligochaeta* in the vegetational belts of the delta of Sannarån 1949. (For symbols, see Fig. 8).

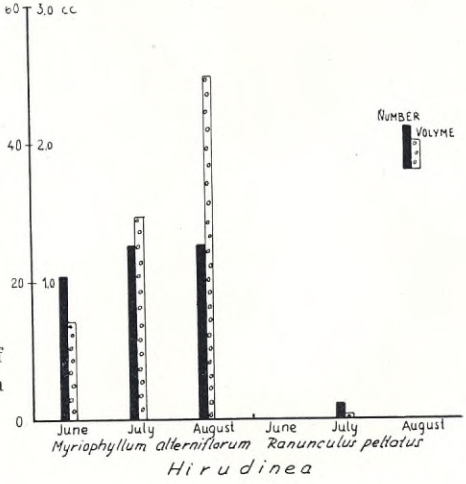

Fig. 12. Seasonal changes in the abundance of *Hirudinea* in the vegetational belts of the delta of Sannarån 1949. (For symbols, see Fig. 8).

Table I. Epifauna on *Carex vesicaria;* the delta of River Sannarån, summer 1949.

		June					July					August					The whole summer				
Collection months		June					July					August					The whole summer				
Number of samples		16					15					16					47 (total)				
Washed weight (kg) ... K		2.02					2.19					2.00					6.21 (total)				
Total number of organisms N		304					30					33					367 (total)				
Number of organisms per kg (washed weight) ... $\frac{N}{K}$		150.5					13.7					16.5					60.2 (average)				
Total volume of organisms (cc) ... V		6.84					2.32					3.56					12.72 (total)				
Volume of organisms per kg (washed weight) ... $\frac{V}{K}$		3.39					1.06					1.78					6.23 (average)				
			$\frac{A}{K}$	$\frac{B}{K}$	C	D		$\frac{A}{K}$	$\frac{B}{K}$	C	D		$\frac{A}{K}$	$\frac{B}{K}$	C	D		$\frac{\Sigma A}{3}$	$\frac{\Sigma B}{3}$	E	F
Oligochaeta	Tubifex sp.	A 15 B 0.73	7.4	0.36	4.9	10.7	A 4 B 0.20	1.8	0.09	13.3	8.6	A 12 B 1.49	6.0	0.75	36.4	41.8	Σ A 15.2 Σ B 1.20	5.1	0.40	8.4	0.7
	Lumbriculus sp.	—	—	—	—	—	A 3 B 0.02	1.4	0.01	10.0	0 9	—	—	—	—	—	Σ A 1.4 Σ B 0.01	0.5	0.003	0.8	0.2
Phyllopoda	Eurycercus lamellatus	A 31 B 0.11	15.3	0.05	10.2	1.6	—	—	—	—	—	—	—	—	—	—	Σ A 15.3 Σ B 0.05	5.1	0.04	8.4	0.9
Malacostraca	Gammarus lacustris Sars	A 3 B 0.15	1.5	0.07	1.0	2.2	—	—	—	—	—	—	—	—	—	—	Σ A 1.5 Σ B 0.07	0.5	0.02	0.8	1.2
Ephemeroptera	Baëtis sp.	A 179 B 1.87	88.6	0.93	58.9	27.3	—	—	—	—	—	—	—	—	—	—	Σ A 88.6 Σ B 0.93	29.5	0.31	48.8	14.7
	Siphlurella sp.	A 43 B 2.76	21.3	1.37	14.1	40.4	A 6 B 0.48	2.7	0.22	20.0	20.7	A 8 B 1.01	4.0	0.51	24.2	28.3	Σ A 28.0 Σ B 2.10	9 3	0.7	15.5	33.4
Trichoptera	Cyrnus flavidus	A 3 B 0.07	1.5	0.03	1.0	1.0	A 5 B 0.11	2.3	0.05	16.7	4.7	A 8 B 0.19	4.0	0.1	24.2	5.3	Σ A 7.8 Σ B 0.18	2.6	0.06	4.4	2.9
	Limnophilus sp.	A 3 B 0.21	1.5	0.10	1.0	3.1	A 6 B 1.2	2.7	0.55	20.0	51.7	—	—	—	—	—	Σ A 4.2 Σ B 0.65	1.4	0.22	2.5	11.0
Diptera	Pentaneura sp.	—	—	—	—	—	A 3 B 0.04	1.4	0.02	10.0	1.7	—	—	—	—	—	Σ A 1.4 Σ B 0.02	0.5	0.01	0.8	0 3
	Cricotopus sp.	A 3 B 0.03	1.5	0.02	1.0	0.4	—	—	—	—	—	—	—	—	—	—	Σ A 1.5 Σ B 0.02	0.5	0.01	0.8	0.2
	Psectrocladius sp.	A 6 B 0.04	3.0	0.02	2.0	0.6	—	—	—	—	—	—	—	—	—	—	Σ A 3.0 Σ B 0.02	1.0	0.01	1.6	0.3
Coleoptera	Dytiscus marginalis	—	—	—	—	—	A 1 B 0.04	0.5	0.02	3.3	1.7	A 1 B 0.04	0.5	0.02	3.0	1.1	Σ A 1.0 Σ B 0.04	0.3	0.01	0.5	0.6
Gastropoda	Gyraulis acronicus	A 18 B 0.87	8.9	0.43	5.9	12.7	A 2 B 0.23	0.9	0.11	6.7	9.9	A 4 B 0.83	2.0	0.42	12.1	23.3	Σ A 11.8 Σ B 0.96	3.9	0.32	6.5	15.2

A=Number of organisms.
B=Volume of organisms.
C=Percent of all organisms by number taken during the same month.
D=Percent of all organisms by volume taken during the same month.
E=Percent of all organisms by number taken during three months.
F=Percent of all organisms by volume taken during three months.

Table II. Epifauna on *Myriophyllum alterniflorum:* the delta of River Sannarån, summer 1949.

Collection months		June					July					August					The whole summer				
Number of samples		50					60					60					170 (total)				
Washed weight (kg) ... K		3.20					9.03					8.35					20.58 (total)				
Total number of organisms N		1650					5600					4860					12110 (total)				
Number of organisms per kg (washed weight) ... $\frac{N}{K}$		515.6					620.1					582.0					1717.7 (total) 572.5 (average)				
Total volume of organisms (cc) ... V		88.0					182.5					172.3					442.8 (total)				
Volume of organisms per kg (washed weight) ... $\frac{V}{K}$		27.5					20.2					20.6					68.3 (total) 22.8 (average)				
			$\frac{A}{K}$	$\frac{B}{K}$	C	D		$\frac{A}{K}$	$\frac{B}{K}$	C	D		$\frac{A}{K}$	$\frac{B}{K}$	C	D		$\frac{\Sigma A}{3}$	$\frac{\Sigma B}{3}$	E	F
Oligochaeta	Tubifex sp.	A 351 B 8.8	109.6	2.75	21.3	10.0	A 1247 B 35.9	138.1	3.97	22.4	19.7	A 243 B 16.2	29.1	1.94	5.0	9.4	Σ A 276.3 Σ B 8.66	92.1	2.55	15.2	13.8
	Lumbriculus sp.	A 36 B 2.1	11.3	0.66	2.2	2.4	A 93 B 9.6	10.3	1.06	1.7	5.3	—	—	—	—	—	Σ A 21.6 Σ B 1.72	7.2	0.57	1.1	2.6
Hirudinea	Helobdella stagnalis L.	A 67 B 2.3	20.9	0.72	4.1	2.6	A 229 B 13.3	25.4	1.47	4.1	7.3	A 207 B 20.6	24.8	2.47	4.3	11.9	Σ A 71.1 Σ B 4.66	23.7	1.55	4.2	8.2
Phyllopoda	Eurycercus lamellatus Müll.	A 9 B 0.1	2.8	0.03	0.5	0.01	A 1336 B 11.1	148.0	1.23	23.9	6.1	A 2540 B 17.6	304.2	2.11	52.3	10.2	Σ A 455.0 Σ B 3.37	151.7	1.12	32.1	6.5
Malacostraca	Gammarus lacustris Sars	A 57 B 8.0	17.8	2.50	3.5	0.9	A 152 B 15.8	16.8	1.75	2.7	8.7	A 283 B 29.2	33.9	3.5	5.8	16.9	Σ A 68.5 Σ B 7.75	22.8	2.58	4.1	12.0
Acarina	Hydracarina	—	—	—	—	—	A 91 B 2.5	10.1	0.28	1.6	1.4	A 53 B 3.6	6.35	0.43	1.1	2.1	Σ A 16.5 Σ B 0.71	5.5	0.23	1.2	1.4
Plecoptera	Nemura sp.	A 7 B 1.1	2.2	0.3	0.4	1.3	A 63 B 6.4	6.97	0.71	1.1	3.5	A 9 B 0.8	1.08	0.1	0.2	0.4	Σ A 10.3 Σ B 1.11	3.4	0.37	0.7	1.9
Ephemeroptera	Baëtis sp. Siphlurella sp. Siphlonurus sp. Cloëon sp.	A 73 — A 453 —	164.4	6.8	31.9	24.8	A 293 A 17 A 631 A 19	106.3	3.37	17.1	16.7	A 326 A 153 A 161 —	76.6	5.64	13.2	27.3	Σ A 347.3 Σ B 15.8	115.8	5.3	17.6	22.4
Neuroptera	Sialis sp.	A 9 B 3.2	2.8	1.0	0.5	3.6	A 9 B 4.1	1.0	0.5	0.2	2.2	—	—	—	—	—	Σ A 3.8 Σ B 1.5	1.3	0.5	0.1	0.6

Table II. Continued.

Trichoptera	Polycentropus flavomaculatus Pict.	—	—	—	—	—	A 19 B 1.1	2.1	0.12	0.3	0.6	—	—	—	—	—	Σ A 2.1 Σ B 0.12	0.7	0.04	0.2	0.2
	Halesus tesselatus	A 43 B 4.5	13.4	1.41	2.6	5.1	A 45 B 5.4	4.98	0.6	0.8	3.0	—	—	—	—	—	Σ A 18.4 Σ B 2.0	6.1	0.67	7.3	2.2
	Cyrnus flavidus	A 51 B 5.3	15.9	1.65	3.1	6.0	A 73 B 8.2	8.08	0.91	1.3	4.5	A 57 B 8.5	6.82	1.02	1.2	4.9	Σ A 30.8 Σ B 3.58	10.3	1.19	1.5	4.9
	Rhyacophila nubila	—	—	—	—	—	A 18 B 1.1	2.0	0.12	0.4	0.6	A 9 B 0.9	1.08	0.108	0.2	0.5	Σ A 3.07 Σ B 0.23	1.0	0.08	0.2	0.5
	Limnophilus sp.	—	—	—	—	—	A 9 B 0.5	1.0	0.06	0.2	0.03	—	—	—	—	—	Σ A 1.0 Σ B 0.06	0.3	0.02	0.07	0.1
	Molanna angustata	—	—	—	—	—	A 9 B 2.1	1.0	0.23	0.2	1.2	—	—	—	—	—	Σ A 1.0 Σ B 0.23	0.3	0.08	0.07	0.5
	Hydropsyche sp.	—	—	—	—	—	A 9 B 2.0	1.0	0.23	0.2	1.1	—	—	—	—	—	Σ A 1.0 Σ B 0.23	0.3	0.08	0.07	0.5
	Stenophylax stellatus	—	—	—	—	—	—	—	—	—	—	A 29 B 3.2	3.47	0.38	0.6	1.9	Σ A 3.47 Σ B 0.38	1.2	0.14	0.2	0.7
	Pryganea striata	—	—	—	—	—	—	—	—	—	—	A 27 B 4.0	3.23	0.48	0.6	2.3	Σ A 3.23 Σ B 0.48	1.1	0.16	0.2	0.9
Diptera	Pentaneura Prodiamesa Heterotrissocladius Cricotopus Psectrocladius Chir. Thummigr Tanytarsus greg gr Simulium sp.	A 173 — — A 9 — A 19 — A 8	65.3	0.7	12.7	0.3	A 147 — A 173 A 293 A 427 A 27 A 9 A 7	120.0	1.3	19.3	6.1	A 73 A 41 A 37 A 92 A 231 — — —	56.7	0.6	9.8	2.7	Σ A 242.0 Σ B 2.6	80.7	0.86	14.5	3.9
Coleoptera	Dytiscus marginalis	—	—	—	—	—	—	—	—	—	—	A 17 B 1.1	2.0	0.1	0.3	0.6	Σ A 2.0 Σ B 0.1	0.7	0.03	0.1	0.2
Gastropoda	Valvata macrostoma	A 19 B 2.1	5.9	0.7	1.2	2.4	A 9 B 1.5	1.0	0.2	0.2	0.8	—	—	—	—	—	Σ A 6.9 Σ B 0.9	2.3	0.3	0.2	0.8
	Limnaea peregra	A 9 B 1.7	2.8	0.5	0.5	1.9	—	—	—	—	—	—	—	—	—	—	Σ A 2.8 Σ B 0.5	0.9	0.2	0.1	0.4
	Gyraulis acronicus	A 173 B 13.5	54.1	4.2	10.5	14.8	A 65 B 6.1	7.2	0.7	1.2	3.3	A 263 B 15.4	31.5	1.8	5.4	0.9	Σ A 92.8 Σ B 6.7	30.9	2.2	2.7	5.7
Lamellibranchiata	Pisidium sp.	A 84 B 11.2	26.3	4.2	5.1	12.7	A 81 B 13.7	9.0	1.5	1.4	7.5	A 9 B 0.2	1.1	0.02	0.2	0.1	Σ A 36.4 Σ B 5.7	12.1	1.9	1.4	5.7

A=Number of organisms.
B=Volume of organisms.
C=Percent of all organisms by number taken during the same month.
D=Percent of all organisms by volume taken during the same month.
E=Percent of all organisms by number taken during three months.
F=Percent of all organisms by volume taken during three months.

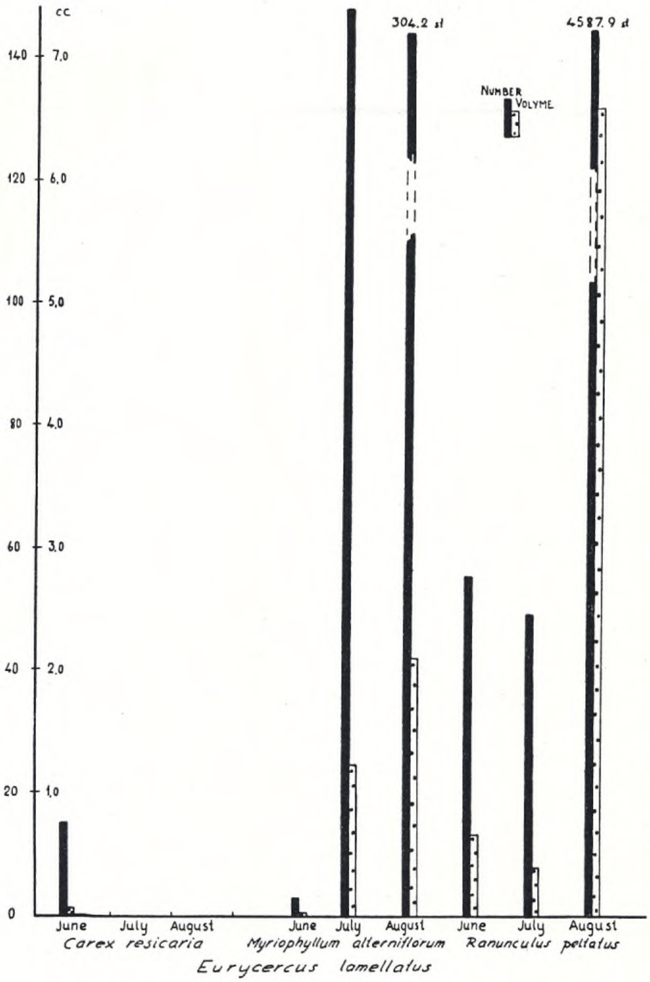

Fig. 13. Seasonal changes in the abundance of *Eurycercus lamellatus* in the vegetational belts of the delta of Sannarån 1949. (For symbols, see Fig. 8).

Fig. 12 and Table II show that in June we have to do with younger individuals which grow with the rising temperature of the water. It seems as if only one generation were formed during the summer. This, according to BOISEN-BENNIKE, agrees with Alpine conditions.

No specimens have been found upon *Carex vesicaria,* but *Carex* does neither carry such a rich fauna of chironomids and snails. *Helobdella stagnalis* lives on larvae of chironomids, snails, worms, and *Asellus aquaticus* (BOISEN-BENNIKE 1943).

Phyllopoda.

Eurycercus lamellatus (MÜLL.) (Fig. 13).

If we study the monthly diagrams (Fig. 13, Tables I, II, and III) for *Eurycercus lamellatus* from the delta of Sannarån, we notice that during

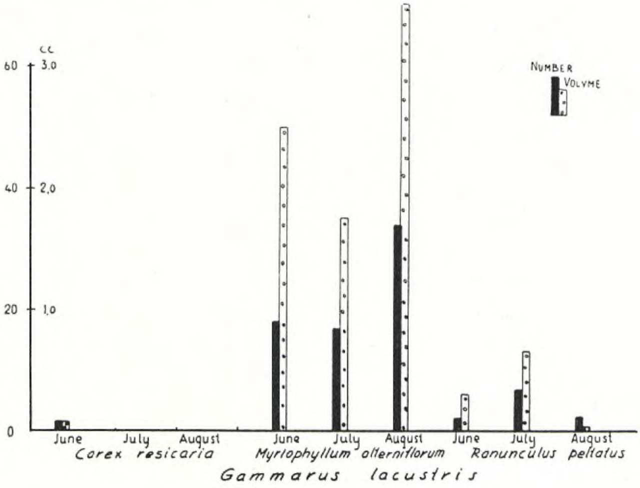

Fig. 14. Seasonal changes in the abundance of *Gammarus lacustris* in the vegetational belts of the delta of Sannarån 1949. (For symbols, see Fig. 8).

June this animal is distributed over all three vegetational regions with a preponderance for that of *Ranunculus peltatus*. *Carex vesicaria* had, as already pointed out, few epiphytes, neither does it offer to *Eurycercus* equally good hiding places as the other plants. In July and August *Eurycercus* has disappeared from *Carex vesicaria*, and is instead found richly represented in the two other vegetational belts.

The largest animals are found in July in the *Myriophyllum* belt. They probably represent the first generation of the summer that has become full-grown (see EKMAN 1904, LANGHANS 1911). WEIGOLD (1914) has shown *Eurycercus* to be dependent on a rich supply of food, while the females carry embryos. Most of the females with embryos in the brood chamber were encountered at the end of July and the beginning of August in the *Myriophylum* belt which was richest in epiphytes, and also by its density could offer good cover.

During August the greatest number of *Eurycercus* are found upon *Ranunculus peltatus*. These are small animals; compare the volume in Table III for August with the volume for July. They are newly hatched animals which have settled down here.

In spite of the fact that the number of animals is about ten times larger upon *Ranunculus peltatus* in August than upon *Myriophyllum alterniflorum* during the same month, it is nevertheless not possible to say that *Eurycercus* should actively seek out *Ranunculus* rather than *Myriophyllum*. This is contradicted by the distribution in July.

Many factors could be thought of to interfere, e.g. the differences in anatomy and habitus of the plants in question; see Fig. 6 a and 6 b. There we see that *Ranunculus* has some kind of spiny processes which are missing in *Myriophyllum* (Fig. 7 a and 7 b). It is imaginable that these processes

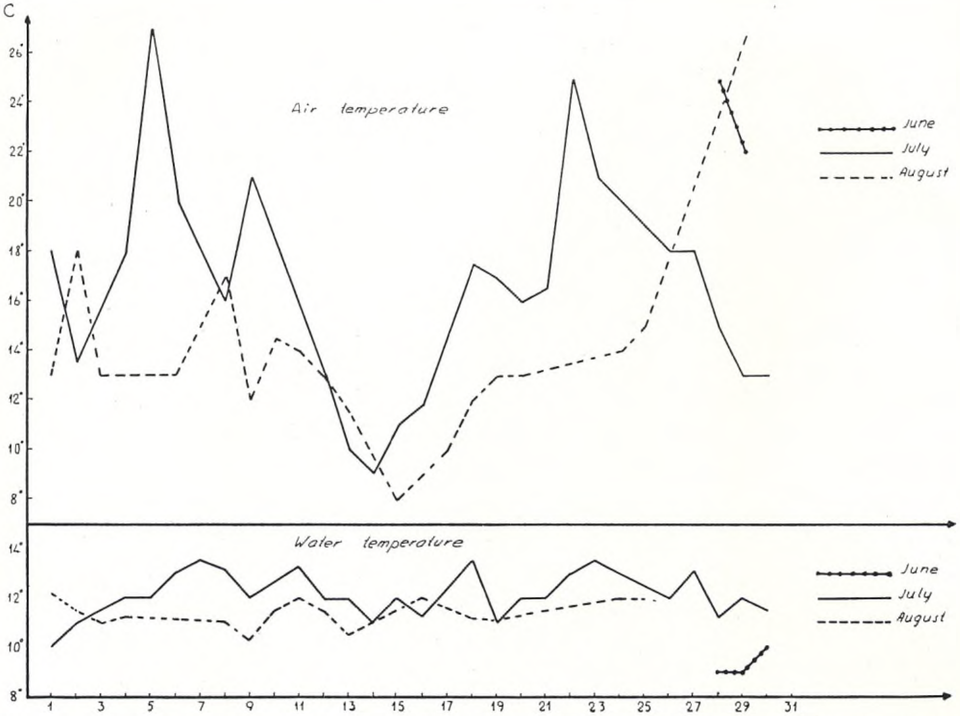

Fig. 15. The air and water temperature at 12 o'clock noon in the delta of Sannarån 1949.

have acted as a kind of sieve, and have caught the young animals which there have found an easier hold for antennae and the crest of the shell (Weigold 1914). Most of the animals, generally of very small size, have been found just around these processes. Between the four processes at the top we see a gathering of epiphytes (Fig. 6 b) which could also have acted as attractions.

Amphipoda.

Gammarus lacustris (Fig. 14).

In northern Europe two species, viz. *Gammarus pulex* (L.) and *Gammarus lacustris* (G. O. Sars) are found (Schellenberg 1934).

In quite a number of papers these two species have been confused, but an investigation by Segerstråle (1954) has cleared up matters as far as northern Europe is concerned.

A study of Fig. 14 and of Tables I, II, and III shows *Gammarus lacustris* in the delta of Sannarån to be represented in June upon all plants examined, the greatest number per kilogram of plants being found upon *Myriophyllum*. According to Dahl's investigation in Norway (1915, Dahl's *G. pulex* is probably *G. lacustris* according to Segerstråle (1954)) we ought to have to do here mainly with full-grown individual (as is corroborated also by the

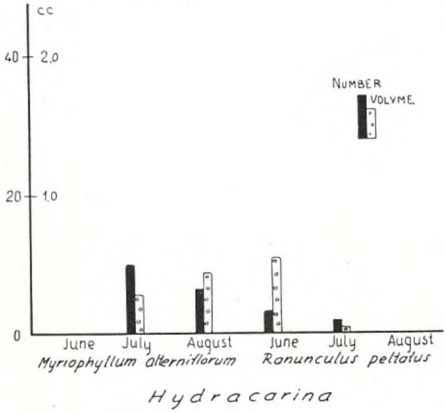

Fig. 16. Seasonal changes in the abundance of *Hydracarina* in the vegetational belts of the delta of Sannarån 1949. (For symbols, see Fig. 8).

ratio of volume to number of individuals) together with some younger individuals.

During July and August no individuals were found in the *Carex* belt. Upon *Myriophyllum* the number of individuals per kilogram of plants is nearly the same in June and July, but reaches the double in August. Upon *Ranunculus peltatus* on the other hand we observe an increase in the number of individuals per kilogram of plants during July, followed by decrease during August until the figures for June are reached.

In comparison with June the temperature of the water rises in July and August (Fig. 15). According to STÅLBERG (1941) the females of *Gammarus* are sensitive to high temperatures, and this fact may constitute one of causes for the disappearance of *G. lacustris* from the *Carex* belt which, growing in shallower water, is more quickly warmed up. The belts of *Myriophyllum* and *Ranunculus* becoming increasingly denser during July and August, supply better shelter to the gammarids and their growing brood, and at the same time offer, compared with the *Carex* region, a greater store of food suitable for *G. lacustris*. The food consists of fresh plants, especially filiform algae, plant detritus, copepods, mysids, and larvae of mussles. (SEGERSTRÅLE 1944). The food is ingested by active as well as by passive filtration (PONYI 1956). Besides, the *Ranunculus* belt contains in August very few animals per kilogram of plants. Compared with the others this belt occupies a more exposed position (see Fig. 3), and *G. lacustris* prefers, according to STÅLBERG (1941) fairly quiet water.

Copepoda.

Heterocope saliens (LILJEB.) (Table III).

Only some isolated specimens were found in the samples from the *Ranunculus* belt. They are not epibionts, but do not avoid shallow water. In the course of his investigations in the mountains of northern Sweden EKMAN (1904) has found *Heterocope saliens* fairly frequently in small ponds and pools.

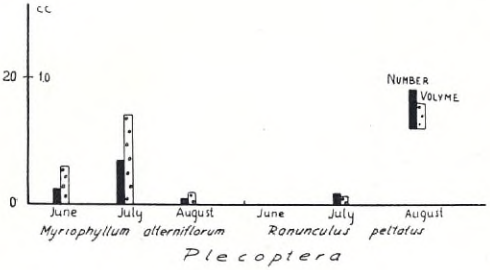

Fig. 17. Seasonal changes in the abundance of *Plecoptera* in the vegetational belts of the delta of Sannarån 1949. (For symbols, see Fig. 8).

Acarina.

Hydracarina (Fig. 16).

According to VIETS (1924) the hydracarines perform in the lakes periodical migrations in vertical direction. In northern Germany they attain during the middle of the summer the highest frequency in shallow water. After a decrease in their numbers they descend lower down during the cooler season, in order to return against spring in increasing numbers towards the littoral.

The samples from the delta of Sannarån agree with these statements. During the middle of the summer they show a decided maximum of frequency.

According to the histogram of the *Myriophyllum* region the animals grow in size during August, when their number has decreased. In August they have disappeared from the other plants, having probably descended, in accordance with the foregoing, into deeper water.

Plecoptera.

Nemura sp. (Fig. 17, Tables II and III).

In the delta of Sannarån (Fig. 17, Tables II and III) the greatest number of plecopteres are found upon *Myriophyllum alterniflorum* and *Ranunculus peltatus,* respectively, in July, a minimum being observed in August. According to BRINCK (1949) this ought to agree with the swarming of the imagines in July. In this place of examination no plecopteres have been discovered upon *Carex vesicaria.* The temperature is probably too high to suit them (BRINCK 1949), besides the epiphytes are not numerous here.

According to BRINCK the food of *N. cinerea* consists mainly of particles of plants, detritus, mineral matter, diatoms, and green algae. They are consequently phytophagous. The nymphs of the Swedish plecopteres feed during the darker periods of the day. During daylight they hide under stones or in the vegetation (BRINCK 1949). *Myriophyllum* offers better hiding places than *Ranunculus.* Upon *Ranunculus* mostly smaller animals are found in July. (The column for numbers is higher than the column representing volume.) Also in the foregoing *Ranunculus* has shown to harbour smaller individuals, e.g. *Eurycercus lamellatus.*

Ephemeroptera. (Fig. 18.)

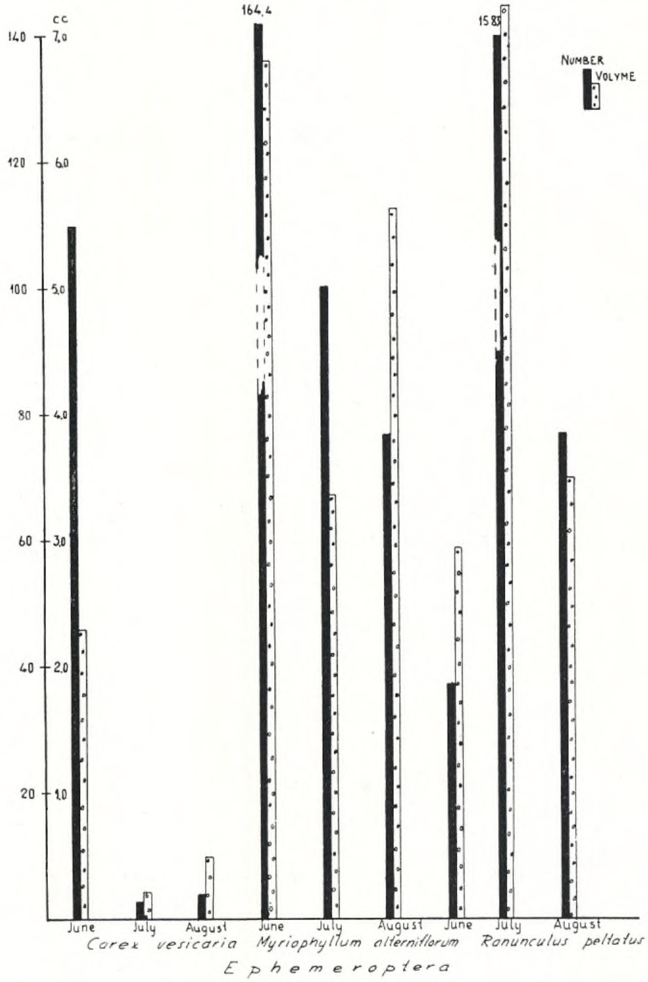

Fig. 18. Seasonal changes in the abundance of *Ephemeroptera* in the vegetational belts of the delta of Sannarån 1949. (For symbols, see Fig. 8).

According to Tables I, II, and III four genera are found to be represented in the delta of Sannarån. Among them *Baëtis sp.,* which was most numerous, and *Siphlurella sp.* occurred upon all the three compared plants. *Siphlonurus sp.,* which comes next in frequency to *Baëtis,* and *Cloëen sp.* which is represented only by a small number, occurred, however, only upon *Myriophyllum.* According to EATON (1883—1888, p. 11) the stem of *Ranunculus,* when broken, gives off a matter which is poisonous to ephemerids. *Ranunculus* harbours, nevertheless, during the summer a great number of ephemerids, especially Baëtis sp.

In the epifauna of the delta the greatest number of larvae is found in June (Fig. 18). Afterwards a continuous decrease in number takes place, if the epifauna of all plants is added up month by month. If, however, a comparison is made between the plants, the conditions are different. In June the number of ephemerids per 1 kg. of plant substance is greater upon *Carex* than upon *Ranunculus,* while in July the conditions are reversed. The supply of epiphytes upon *Carex* was probably not satisfactory. From July to August the *Carex* belt exhibits an increase in the number of ephemerids, whereas a reduction takes place in the two other vegetational zones. *Carex vesicaria* also grows in the shallowest places, and reaches above the surface of the water. For this reason it is imaginable that there the increase in numbers is due to larvae which are ready for the stage of subimago, and which therefore creep above the surface of the water in order to reach the stage of imago. We also find the column for the volume to be twice as large as the column for the numbers, which confirms that we have to do with larger and older animals. Otherwise we find that the ephemerids grow in the course of the summer, and that most of them seem to swarm during August with the beginning in July. In August we find that *Ranunculus* in addition carries also smaller animals. According to BERG (1948) these can be *Baëtis sp.* which have hatched late from hibernating eggs, and therefore have supplied a contribution of young animals, or they might be derived from eggs which had been newly laid during the summer. *Cloëon sp.* appears only during July, and then in small numbers. Its swarming period has probably already passed. *Cloëon praetextum* MIHI e.g. swarms, according to BENGTSSON (1914), in June—August.

From the point of view of nutrition the plants in the delta of Sannarån offer to the different genera of ephemerids very suitable dwelling places.

The mouth parts of the larvae are masticatory to biting. Many scientists (PICTET 1843, EATON 1888, etc.) have therefore concluded that the larvae should feed on both animalic and vegetabilic substances. WISSMEYER (1926) has performed feeding experiments with larvae of certain ephemerids. In doing so he found e.g. in experiments with *Cloëon* and *Ephemerella* that they are mainly herbivorous, and that *Cloëon* consumed animalic food (copepods, daphnids) only, when no plants were available. *Ephemerella,* on the other hand, could consume mixed food, with a preponderance of vegetable substances. Plants with a multitude of green algae and diatoms are especially tempting. WISSMEYER (1926) also noticed that the vegetable substance left the body of the animal without being wholly digested. According to REHBRONN (1937) *Siphlonurus sp.* and *Baëtis sp.* support themselves in the same way as *Cloëon.* In species which were dwelling upon *Potamogeton perfoliatus* he found rests of cocconeids, gomphonemids, and diatoms.

Neuroptera. (Fig. 19.)

Sialidae.

They are found in the delta of Sannarån upon *Myriophyllum alterniflorum,* where the fauna of oligochaetes was richest. The animals feed on pisidiids worms, and larvae of gnats (WESENBERG-LUND 1943).

Table III. Epifauna on *Ranunculus peltatus;* the delta of River Sannarån, summer 1949.

Collection months		June					July					August					The whole summer				
Number of samples		20					25					30					75 (total)				
Washed weight (kg)...........K		2.04					3.33					2.07					7.44 (total)				
Total number of organisms N		492					752					9719					10963 (total)				
Number of organisms per kg (washed weight) ... N/K		241.2					225.8					4695.2					5162.2 (total) 1720.7 (average)				
Total volume of organisms (cc) V		9.02					28.56					23.31					60.89 (total)				
Volume of organisms per kg (washed weight) ... N/V		4.42					8.58					11.26					24.26 (total) 8.09 (average)				
			A/K	B/K	C	D		A/K	B/K	C	D		A/K	B/K	C	D		ΣA/3	ΣB/3	E	F
Oligochaeta	Tubifex sp.	A 11 B 0.49	5.4	0.24	2.2	5.4	A 22 B 0.57	6.6	0.17	2.9	2.0	—	—	—	—	—	Σ A 12.0 Σ B 0.41	4.0	0.13	0.3	1.7
Hirudinea	Helobdella stagnalis	—	—	—	—	—	A 4 B 0.1	1.2	0.03	0.5	0.4	—	—	—	—	—	Σ A 1.2 Σ B 0.03	0.4	0.01	0.04	0.2
Phyllopoda	Eurycercus lamellatus	A 113 B 1.39	55.4	0.68	23.0	15.4	A 165 B 1.32	49.6	0.40	21.9	4.6	A 9497 B 13.7	4587.9	6.62	97.7	58.8	Σ A 4692.9 Σ B 7.70	1564.3	2.57	89.2	27.0
Malacostraca	Gammarus lacustris Sars	A 4 B 0.63	2.0	0.31	0.8	7.0	A 23 B 2.19	6.9	0.66	3.1	7.7	A 5 B 0.09	2.4	0.04	0.05	3.9	Σ A 11.3 Σ B 1.01	3.8	0.33	0.3	4.8
Copepoda	Heterocope saliens	—	—	—	—	—	—	—	—	—	—	A 7 B 0.11	3.4	0.05	0.07	0.5	Σ A 3.4 Σ B 0.05	1.1	0.02	0.06	0.2
Acarina	Hydracarina	A 6 B 0.11	2.9	0.54	1.2	1.2	A 5 B 0.06	1.5	0.02	0.7	0.2	—	—	—	—	—	Σ A 4.4 Σ B 0.56	1.5	0.19	0.1	0.3
Plecoptera	Nemura sp.	—	—	—	—	—	A 6 B 0.22	1.8	0.07	0.8	0.8	—	—	—	—	—	Σ A 1.8 Σ B 0.07	0.6	0.02	0.05	0.4
Ephemeroptera	Baëtis sp.	A 306 B 4.7	15.0	2.30	62.2	52.1	A 330 B 11.3	99.1	3.39	43.9	39.6	A 158 B 7.15	76.3	3.45	1.6	30.7	Σ A 325.4 Σ B 9.14	108.5	3.05	7.2	38.0
	Siphlurella sp.	A 46 B 1.3	22.5	0.64	9.3	14.4	A 197 B 12.8	59.2	3.84	26.2	44.8	A 1 B 0.05	0.5	0.02	0.01	0.2	Σ A 82.2 Σ B 4.50	27.4	1.50	2.2	23.2
Trichoptera	Holocentrop sp.	—	—	—	—	—	—	—	—	—	—	A 5 B 0.07	2.4	0.03	0.05	0.3	Σ A 2.4 Σ B 0.03	0.8	0.01	0.05	0.1
	Cyrnus flavidus	—	—	—	—	—	—	—	—	—	—	A 8 B 0.6	3.9	0.29	0.08	2.6	Σ A 3.9 Σ B 0.29	1.3	0.1	0.07	1.0
Diptera	Pentaneura sp.	—	—	—	—	—	—	—	—	—	—	A 6 B 0.03	2.9	0.02	0.06	0.1	Σ B 2.9 Σ A 0.02	1.0	0.01	0.05	0.05
	Psectrocladius sp.	—	—	—	—	—	—	—	—	—	—	A 17 B 0.09	8.2	0.04	0.2	0.4	Σ A 8.2 Σ B 0.04	2.7	0.01	0.2	0.1
	Tanytarsus greg gr	—	—	—	—	—	—	—	—	—	—	A 7 B 0.3	3.4	0.15	0.07	1.3	Σ A 3.4 Σ B 0.15	1.1	0.05	0.06	0.5
Gastropoda	Limnaea peregra	A 6 B 0.4	2.9	0.2	1.2	4.4	—	—	—	—	—	—	—	—	—	—	Σ A 2.9 Σ B 0.2	1.0	0.07	0.05	0.7
	Gyraulis acronicus	—	—	—	—	—	—	—	—	—	—	A 8 B 1.12	3.9	0.54	0.08	4 8	Σ A 3.9 Σ B 0.54	1.3	0.18	0.07	1.8

A=Number of organisms.
B=Volume of organisms.
C=Percent of all organisms by number taken during the same month.
D=Percent of all organisms by volume taken during the same month.
E=Percent of all organisms by number taken during three months.
F=Percent of all organisms by volume taken during three months.

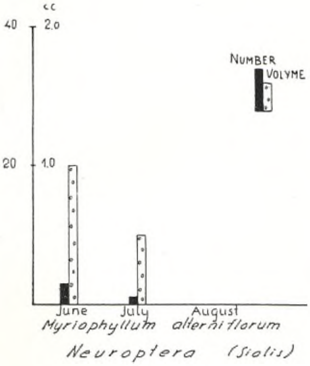

Fig. 19.

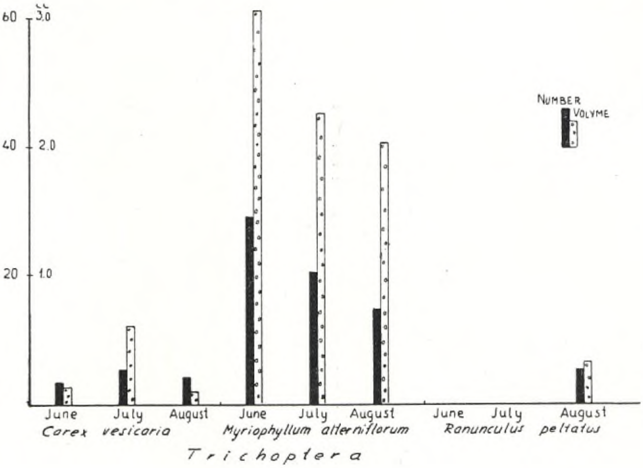

Fig. 20.

Fig. 19. Seasonal changes in the abundance of *Neuroptera* in the vegetational belts of the delta of Sannarån 1949. (For symbols, see Fig. 8).

Fig. 20. Seasonal changes in the abundance of *Trichoptera* in the vegetational belts of the delta of Sannarån 1949. (For symbols, see Fig. 8).

Trichoptera. (Fig. 20)

On studying the distribution of the *Trichoptera* in the examined fauna of the delta (Fig. 20, Tables I, II, and III) we find them represented upon all plants, yet least numerous upon *Ranunculus peltatus.*

Two genera are represented in the *Carex* region. Of them *Limnophilus* seems to swarm earlier. The majority of the species of *Limnophilus* described by ULMER (1909) swarm very early. In August the number of animals had dropped in the *Carex* region, probably in part on account of loss by swarming. In August we find only *Cyrnus flavidus.* Compared with *Limnophilus sp.* the individuals of this species are smaller. This explains the relation between the columns for number and volume (volume=larva without case) in spite of the fact that we probably have to count with fully developed larvae. *Carex vesicaria* supplies good material for the building of the cases of *Limnophilus sp.* (ULMER (1909): plant fragments, sand, shells of molluscs, etc.). With its fairly quiet water and its plants, which also reach above the water, the *Carex* region seems also be a suitable locality for the fixation of the pupae.

Myriophyllum alterniflorum harbours, however, the greatest number of species of *Trichoptera.* This depends certainly upon the fact that this belt, according to the statements about the food in *Siltala* (1907), SLACK (1936), and WESENBERG-LUND (1943), contains the richest supply of food. The number of species culminates in July, and decreases thereafter parallel with their swarming. Here *Stenophylax stellatus* does not appear before August.

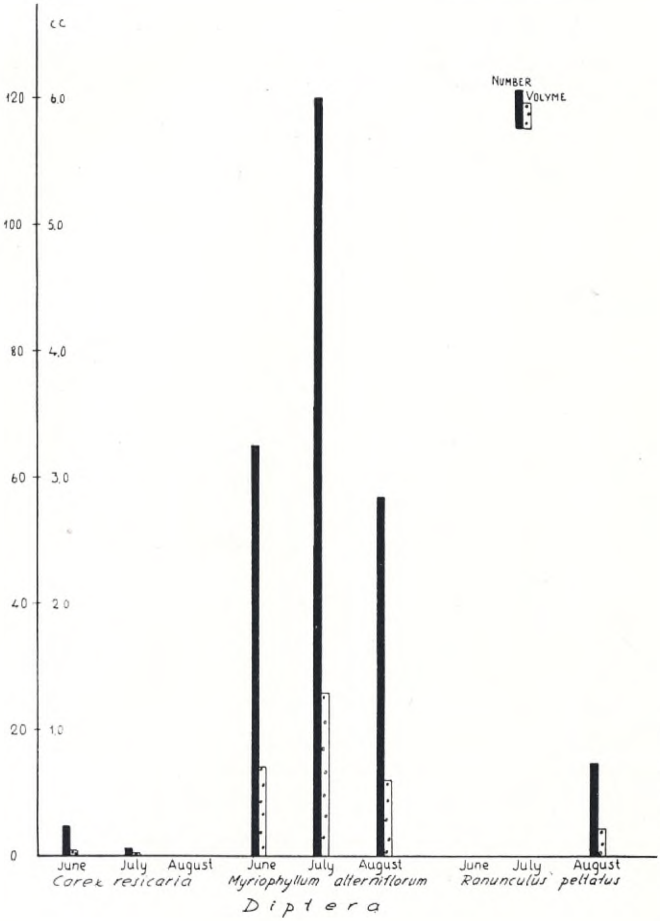

Fig. 21. Seasonal changes in the abundance of *Diptera* in the vegetational belts of the delta of Sannarån 1949. (For symbols, see Fig. 8).

According to Ulmer (1909) it swarms late. According to the same author *Phryganea striata* swarms early. During June and July this species was entirely absent from *Myriophyllum*. The subsequently appearing larvae were so small that they can be thought to be derived from the first hatched generation of the season.

The belt of *Ranunculus* does not seem to constitute a favourable biotope for the *Trichoptera*. The species which have been found upon *Ranunculus peltatus,* viz. *Holocentropus sp.* and *Cyrnus flavidus,* feed according to Siltala (1907) on *Cladocera,* etc. The species found in August in the *Ranunculus* belt have probably been attracted by the maximum frequency of *Eurycercus* at this time in this biotope.

Diptera. (Fig. 21)

In the vegetational belts of the delta of Sannarån larvae belonging to the families *Chironomidae* and *Simulidae* were represented.

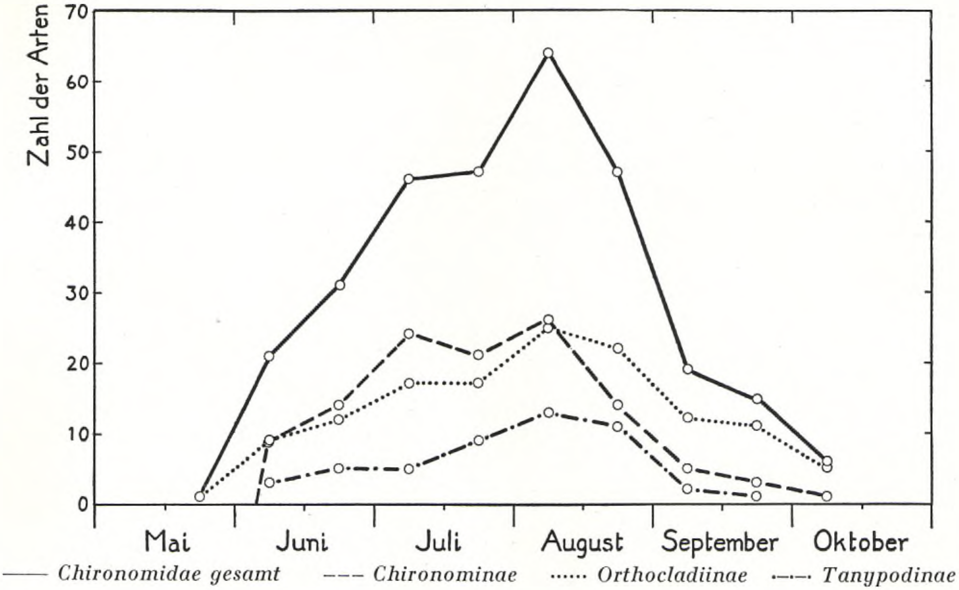

Fig. 22. Seasonal changes in the number of chironomid species emerging in the subarctic lakes of Jämtland. After BRUNDIN 1949.

The frequency of the larvae of *Simulium* was very low. They have certainly been torn from their proper biotope among stones in running water, and carried along with the water, until they got stuck to the plants.

The distribution of the numbers of the chironomids is such that most of the genera are represented upon *Myriophyllum*. In the *Carex* belt only isolated individuals are found, indicating that this biotope does not suit the chironomids particularly well, both epiphytic algae and prey for the carnivors being rare. Some chironomid larvae are carnivorous, especially the larvae of *Tanypus* which possess sharp toothed mandibles (WESENBERG-LUND 1943). Some larvae are filtrators, and usually build tubes. Others again are omnivorous, yet many chironomid larvae are nevertheless herbivorous (WESENBERG-LUND 1943). During the period of investigation the distribution of the chironomids in the *Myriophyllum* belt is rather uniform, with a maximum in July. Most of the species occurring here swarm in August. Some seem to have swarmed also during spring.

Most of the chironomids of our latitudes seem to have a life cycle of one year (THIENEMANN 1954). The imagines swarm once during the warm season, e.g. in spring, summer, or autumn; see Fig. 22 in which BRUNDIN (1949) represents the time of swarming for some chironomids from Jämtland, and Fig. 23 after MEUCHE 1939 in which especially the chironomids of the plant region are entered. The maximum in July (Fig. 21) then consists partly of older animals which are ready for swarming and of growing larvae of the

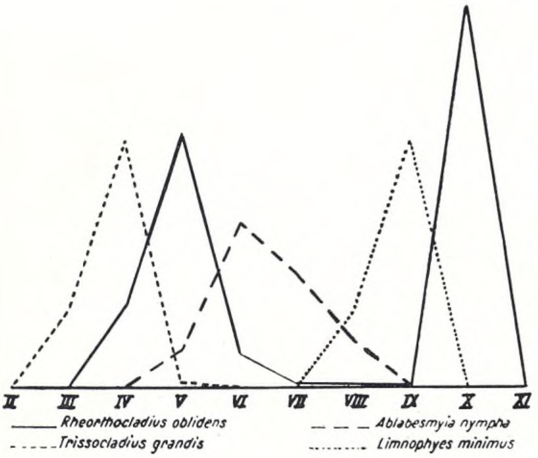

Fig. 23. Seasonal changes in the number of some chironomids from vegetational belts in Lake Plöhn. After MEUCHE 1939.

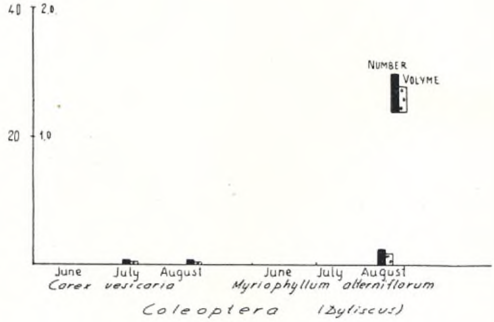

Fig. 24. Seasonal changes in the abundance of *Coleoptera* in the vegetational belts of the delta of Sannarån 1949. (For symbols, see Fig. 8).

species which swarm in spring. The majority of the animals belongs to the orthocladines, followed next among the other chironomids by the tanypodines.

Coleoptera (Fig. 24).

Dytiscus marginalis L.

Dytiscus marginalis is represented only in the *Carex* belt and in the *Myriophyllum* belt. There occur only a few specimens (Tables I and II) on either kind of plant, with a preponderance for *Myriophyllum* in August (Fig. 24). The larvae hatch in early summer, and cling to some plant, often to floating leaves at the edge of the water, where they watch for prey (according to WESENBERG-LUND 1943). In general the examined plants are lacking leaves floating upon the surface of the water. As the larvae of *Dytiscus* live in this way, it is likely that they loose hold during the netting below the surface.

Gastropoda. (Fig. 25).

Among the fauna upon the plants in the delta of Sannarån three species of snails have been found (Tables I—III).

The most important food of the gastropods consists of the algae which cover the higher vegetation, stones, mud, and moldering vegetable substance. The food is not selected, but the snails with their radula scrape whatever comes in their way. By changing the direction they ascend during the warmer season to the surface in order to breathe by means of lungs (*Pulmonata*), and then descend again to the bottom (HUBENDICK 1949).

Fig. 25 shows the gastropods in the delta of Sannarån to be spread over

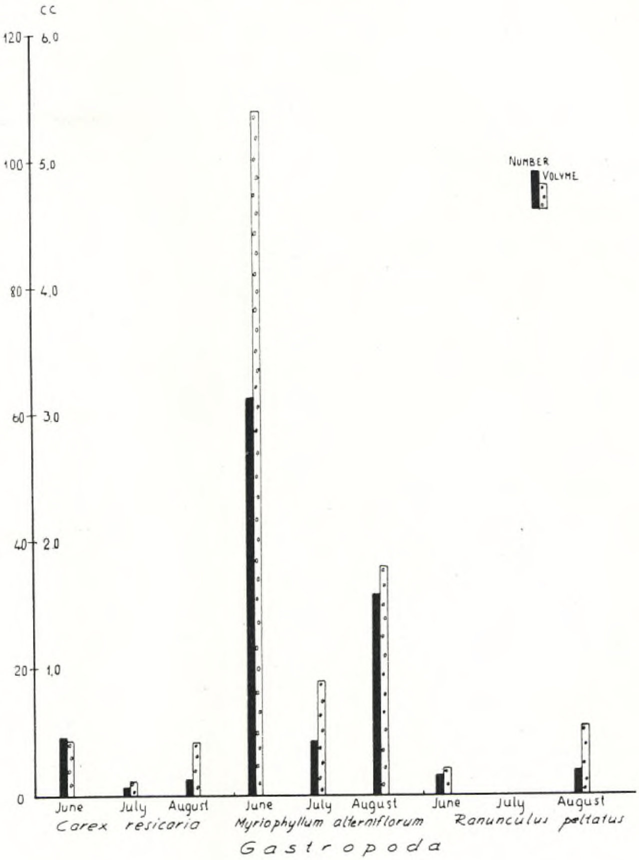

Fig. 25. Seasonal changes in the abundance of *Gastropoda* in the vegetational belts of the delta of Sannarån 1949. (For symbols, see Fig. 8).

all three vegetational regions, with a considerable preponderance for *Myriophyllum alterniflorum*. As far as the order of size (the volume) is concerned it is rather difficult to arrive at any conclusions, the variation in size being very great within one and the same age group (HUBENDICK 1949). If only the number is taken into consideration, the month of June seems to be the richest month upon the majority of plants. We have probably to do with snails from the preceding year which are occupied with the deposition of their eggs (HUBENDICK 1949). In this month also numerous egg cocoons have been found. During July the snails have ascended to the surface in order to breathe by means of their lungs. The majority of the snails (*Gyraulis acronicus*) in the samples belonged to *Pulmonata* (Table II). There existed perhaps a greater probability that the snails sitting at the surface of the water dropped off during the process of netting.

In August the number of the snails exclusively *Gyraulis acronicus*, has again increased. This increase is probably due to the generation produced during the summer which has now hatched, and has started to be included

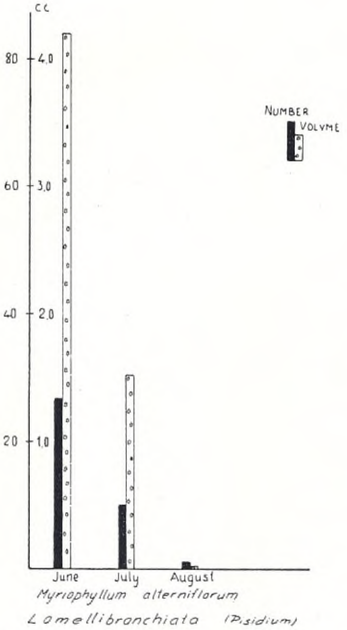

Fig. 26. Seasonal changes in the abundance of *Lamellibranchiata* in the vegetational belts of the delta of Sannarån 1949.

in the samples. The circumstance that in August the samples consisted exclusively of *Gyraulis acronicus* is certainly a consequence of the technical procedure followed in the experiments, since the two other species of snails were very rare during the other months, and could easily drop during the netting.

Valvata macrostoma was found only in the vegetation of *Myriophyllum*. *Gyraulis acronicus* occurred upon all three kinds of plants. *Limnaea peregra* did not occur in the *Carex* belt, but well in the two other belts. The locomotion of the snails is generally not particularly fast. Once an individual has entered a certain area, it will probably remain there during the entire season, provided the food supply does not get exhausted. During the winter the metabolism of the snails is very low (HUBENDICK 1949), and they consume so little oxygen that they need not leave the bottom in order to breathe by means of their lungs.

Lamellibranchiata (Fig. 26).

Pisidium sp.

In the delta of Sannarån *Pisidium sp.* has been found only in the *Myriophyllum* area.

The occurrence of *Pisidium* (Fig. 26) exhibits a maximum in June, and a minimum in August. In June and July we have to do with older individuals with brood. (In June and July the column for the volume is in general much higher han that for the number. In August this difference is less pronounced.) Towards the end of July the animals have probably descended to the bottom, or their numbers may have decreased by enemies and natural death. Since the mussels are fairly loosely attached, it is also conceivable that they have dropped in the process of netting.

In August we have to do with younger animals, probably brood, which, on becoming detached from the mother animal, have remained in the vegetational belt.

3. Bottom Fauna

a. Sedimentary bottoms in 1948 and 1949 (before the regulation).

For the year 1948 there exist only three samples (Table IV) from the north-eastern half of the delta of Sannarån. In this half of the delta most of the sedimentary bottoms are found at a depth of 1 metre.

Table IV. Bottomsamples from the delta of River Sannarån August 1948, June, July and August 1949.

Depth: 1 m 3 × 2.25 dm²	August 12th 1948			June 22th 1949			July 13th 1949			August 15th 1949		
	Number of org.	Org. in % of all org.	Average org. per m²	Number of org.	Org. in % of all org.	Average org. per m²	Number of org.	Org. in % of all org.	Average org. per m²	Number of org.	Org. in % of all org.	Average org. per m²
Oligochaeta	27	40.9	400.0	33	2.2	488.9	117	54.4	1733.3	147	86.0	2177.8
Eurycercus l.	—	—	—	12	0.8	177.8	—	—	—	—	—	—
Polyphemus ped.	—	—	—	1466	96.1	21718.5	—	—	—	—	—	—
Pentaneura sp. ...	—	—	—	—	—	—	18	8.4	266.7	9	5.3	133.3
Heterotrissocl. sp.	—	—	—	15	1.0	222.2	—	—	—	—	—	—
Cricotopus sp.......	27	40.9	400.0	—	—	—	71	33.0	1051.9	12	7.0	177.8
Psectrocladius sp.	—	—	—	—	—	—	—	—	—	3	1.8	44.4
Sergentia sp.	12	18.2	177.8	—	—	—	6	2.8	88.9	—	—	—
Gastropoda sp. ...	—	—	—	—	—	—	3	1.4	44.4	—	—	—
Sum	66	100.0	977.8	1526	100.1	22607.4	215	100.0	3185.2	171	100.1	2533.3

Table V. Bottomsamples from the delta of River Sannarån 16—17th August 1954.

No Depth	I 8 m.			II 8 m.			III 8 m.			IV 9 m.		
10 × 2.25 dm²	Number of org.	Org. in % of all org.	Average org. per m²	Number of org.	Org. in % of all org.	Average org. per m²	Number of org.	Org. in % of all org.	Average org. per m²	Number of org.	Org. in % of all org.	Average org. per m²
Nematodes	—	—	—	61	6.2	271.1	73	39.0	324.4	21	2.3	93.3
Oligochaeta	493	73.3	2191.1	854	86.4	3795.6	52	27.8	231.1	832	90.0	3697.8
Eurycercus lamell.	31	4.6	137.8	—	—	—	—	—	—	—	—	—
Cyclops..............	47	7.0	208.9	—	—	—	—	—	—	—	—	—
Limnophilus sp....	—	—	—	—	—	—	9	4.8	40.0	—	—	—
Pentaneura sp. ...	—	—	—	12	1.2	53.3	41	21.9	182.2	—	—	—
Psectrocladius sp.	—	—	—	11	1.1	48.9	—	—	—	—	—	—
Microtendipes sp.	—	—	—	—	—	—	12	6.4	53.3	—	—	—
Sergentia sp.	102	15.2	453.3	9	0.9	40.0	—	—	—	71	7.7	315.6
Pisidium sp.	—	—	—	41	4.1	182.2	—	—	—	—	—	—
Sum	673	100.1	2991.1	988	99.9	4391.1	187	99.9	831.0	924	100.0	4106.7

59.1 per cent of the animals consisted of chironomids, and 40.9 per cent of oligochaetes, most of them being tubificids. Before the netting in the epifauna could start in 1949 random samples have been taken upon the pure sedimentary bottoms by means of a bottom grab after EKMAN. As this showed that the fauna was not especially abundantly represented there, in the continuation only three samples were taken every month (Table IV).

In the samples from June the main part consists of *Polyphemus pediculus*. According to LILLJEBORG (1900) this animal is often encountered in great clusters, near the shore of larger waters. The animal forms part of the plankton. In this sample the *Oligochaeta* constituted only a few per cent, but were more numerous than the chironomids.

In the samples from July the percentage of the *Oligochaeta* exceeded that of the chironomids by some ten units. These samples contain also an admixture of gastropods.

The samples from August exhibit a strong uppswing of the *Oligochaeta* as compared with the chironomids.

The sedimentation due to the water which passes through the delta of the Sannarån is probably very slow in spite of the fact that the protection by the projecting spits does not permit greater velocities of the water, see Fig. 2 and 3. This conclusion is based upon the rather considerable hardness of the naked sedimentary bottoms. According to ALSTERBERG (1922) the tubificids thrive in mud, rich in detritus, and were also rather few in the hard sediments of the delta, where they nevertheless constituted the most numerous group.

b. Sedimentary bottoms in 1954 (after the regulation).

When the samples were taken (August 16—17, 1954) the level of the damming in Borgasjön was +18 metres (Fig. 27). Now the delta of the Sannarån lay at a dept of 8—13 metres. At the beginning samples were taken spread all over the delta which first had been sounded. Now it was observed that all vegetational areas of 1949 had disappeared, and that gravel, roots of trees, twigs, leaves, and soft sediments had been introduced. The sampling for every metre of the depth, as is otherwise the custom, could not be carried out here, partly because such samples did not prove representative, and partly because the delta still had a fairly smooth bottom, so that not many samples would have been taken in the delta. The sampling of the bottom was therefore carried out in the way described under II: 2 above.

The sampling along the rope mentioned in Chapter II: 2 began in the former *Carex* region at the island in the delta, and was then continued in the direction of the arrow (N—S) along the thickest line which in Fig. 3 repre-

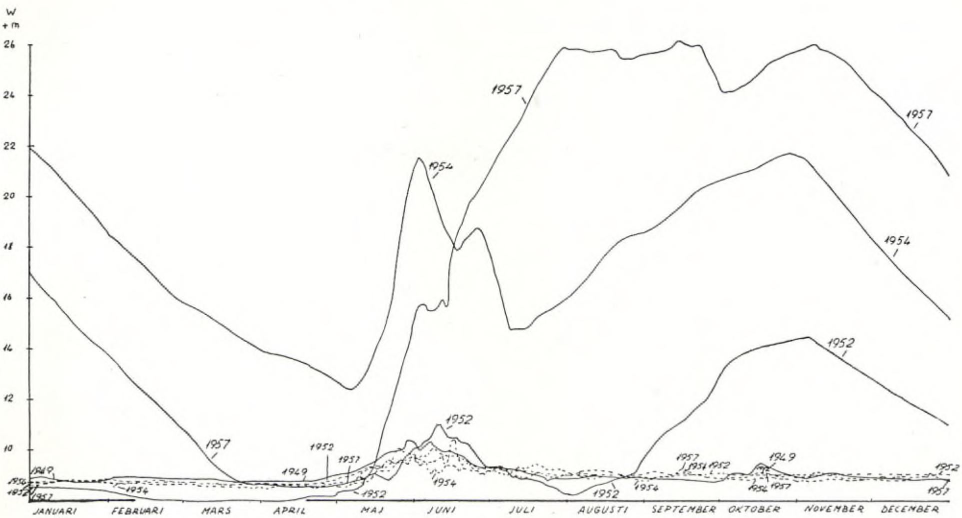

Fig. 27. The seasonal variations in water-level in Lake Borgasjön during 1949, 1952, 1954, and 1957.

sents the rope. For the sake of comparison also ten samples taken at the depth of 3 ms. from the flooded bottoms north of the former delta were examined.

An examination of the Tables V—VII shows that in the majority of the samples the oligochaetes form a very high percentage. Where they are absent, we usually have to do with samples from gravelly bottom. *Eurycercus* is found only in the samples taken at the smallest depth (8 mtrs) towards the northern shore, and outside the former delta.

In many of the samples nematodes occur in fairly great quantities. Great faults can, however, arise here as the result of selection in the sifting through the wire gauze.

Among the chironomids which occur in most of the samples *Sergentia sp.* is the most frequent. In the samples from the depth of 13 ms. the group of *Chironomus thummi* is represented by the greatest numbers.

In samples Nos. I and XV (Tables V and VIII) *Cyclops* and *Daphnia longispina hyalina* are represented. Here these animals do not constitute a high percentage. Neither is this expected, as they have stood as plankton above the bottom.

Helobdella stagnalis occurs only in sample XVI (Table VIII) in which it forms only 4.7 per cent of the animals.

Sample XIV contains some gastropods. They form, however, only 5.4 per cent of the sample which consists preponderately of oligochaetes. Some solitary *Limnophilus sp.* are represented in sample III.

Table VI. Bottomsamples from the delta of River Sannarån 16—17th August 1954.

No Depth	V 9 m.			VI 10 m.			VII 10 m.			VIII 10 m.		
10 × 2.25 dm^2	Number of org.	Org. in % of all org.	Average org. per m^2	Number of org.	Org. in % of all org.	Average org. per m^2	Number of org.	Org. in % of all org.	Average org. per m^2	Number of org.	Org. in % of all org.	Average org. per m^2
Nematodes	94	25.3	417.8	19	2.1	84.4	42	12.5	186.7	—	—	—
Oligochaeta	254	68.5	1128.8	713	77.9	3168.9	171	50.9	760.0	504	100.0	2240.0
Sergentia sp.	23	6.2	102.2	183	20.0	813.3	123	36.6	546.7	—	—	—
Sum	371	100.0	1648.8	915	100.0	4066.6	336	100.0	1493.4	504	100.0	2240.0

Table VII. Bottomsamples from the delta of River Sannarån 16—17th August 1954.

No Depth	IX 12 m.			X 13 m.			XI 13 m.			XII 13 m.		
10 × 2.25 dm^2	Number of org.	Org. in % of all org.	Average org. per m^2	Number of org.	Org. in % of all org.	Average org. per m^2	Number of org.	Org. in % of all org.	Average org. per m^2	Number of org.	Org. in % of all org.	Average org. per m^2
Nematodes	97	53.6	431.1	92	73.0	408.9	—	—	—	—	—	—
Oligochaeta	43	23.8	191.1	23	18.3	102.2	21	70.0	93.3	—	—	—
Sergentia sp.	41	22.7	182.2	11	8.7	48.9	—	—	—	23	5.3	102.2
Chir. Thummi gr.	—	—	—	—	—	—	9	30.0	40.0	412	94.7	1831.1
Sum	371	100.0	1648.8	915	100.0	4066.6	336	100.0	1493.4	504	100.0	2240.0

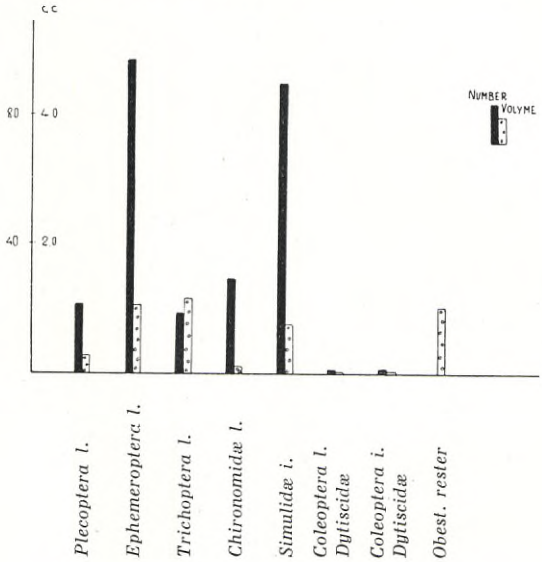

Fig. 28. The food of ten trouts in the delta of Sannarån, June 1949.

4. Fish fauna

The stock of fish in Borgasjön consists of brown trout (*Salmo trutta* L.), char (*Salmo alpinus* L.), burbot (*Lota lota* L.), and minnow (*Phoxinus phoxinus* L.).

Fishing in the delta of Sannarån during the months of sampling in 1949 resulted in trout with sizes between 9.0 and 46.0 cms. (see Table X). The distribution of size was rather uniform between 15 cms. and 31 cms., with an accumulation around fishes of 15—21 cms. length.

The age distribution was such that fishes of 15—25 cms. were 3—5 years, and fishes of 26—30 cms. 5—6 years old.

Of other species of fish only one char and two burbots have been obtained during the course of the summer.

In June 1949 ten stomach samples (Fig. 28) were taken, while in July and August of the same year 100 stomach samples (Figs. 29 and 30) were taken in each month. On comparing in Figs. 28, 29, and 30 the stomach contents of fishes caught in June, July, and August we find the number of represented species to be greatest during the last two months. Since the material for these two months is also larger, the following more detailed comparison will be based mainly upon this material.

In connection with the collection of bottom samples in 1954, i.e. two years after the first damming-up of Borgasjön, an intensive fishing was carried on the delta. As, however, no trout were obtained, no comparison is unfortunately possible between the fauna and the diet of the fish this year.

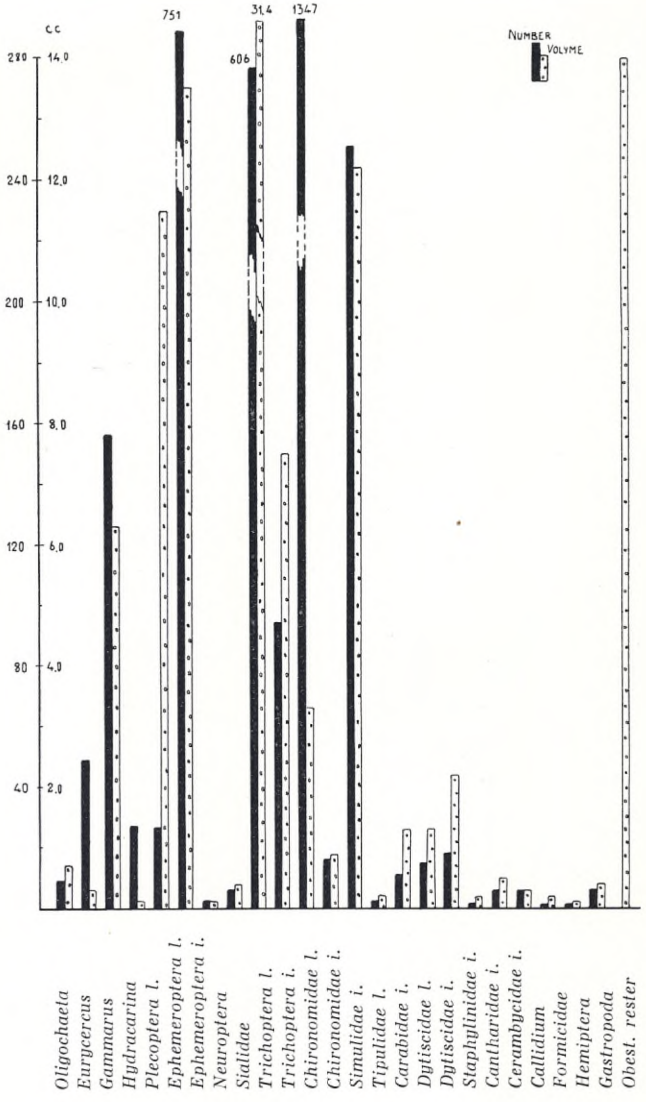

Fig. 29. The food of 100 trouts in the delta of Sannarån, July 1949.

Renewed fishing was carried out in the flooded delta on July 25—26, 1957, i.e. 5 years after the first damming-up. It was observed then that the trout had been almost completely replaced by char which had invaded the delta. The trout, on the other hand, was caught in depths from 1 to 6 metres, thus upon new bottoms, and the char in depths of 6—13 metres. From both trout and char 37 stomach samples were treated. The size of the trout varied between 14.5 and 27.5 cms. The majority fell within the limits 17 and 20 cms.

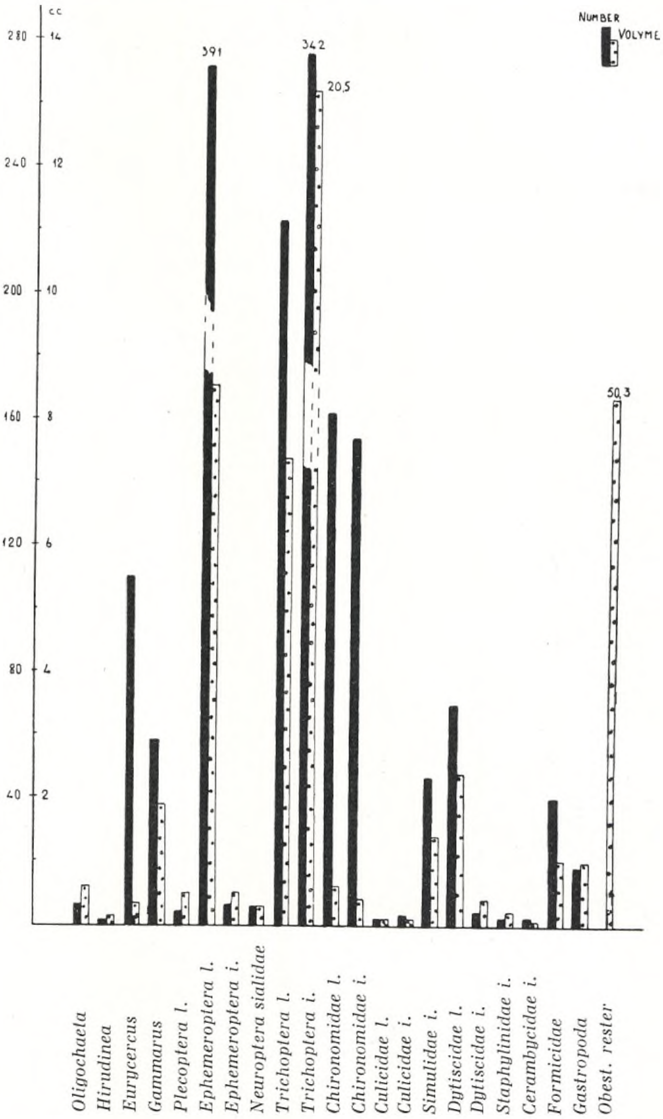

Fig. 30. The food of 100 trouts in the delta of Sannarån, August 1949.

Trout of 14—15 cms. were about 3 summer old, such of 16—18 cms. about 4—5 summers.

The char was represented by sizes between 14.5 cms. and 26.0 cms. Here most of the fishes fall between the limits 15 and 18 cms.

The results of the examinations of the stomach samples are found in Table X, where N=number, V=volume in cc., l=larvae, p=pupae and i=imagines. Percentage of volume is calculated on the basis of the combined stomach content of all fishes of the same kind.

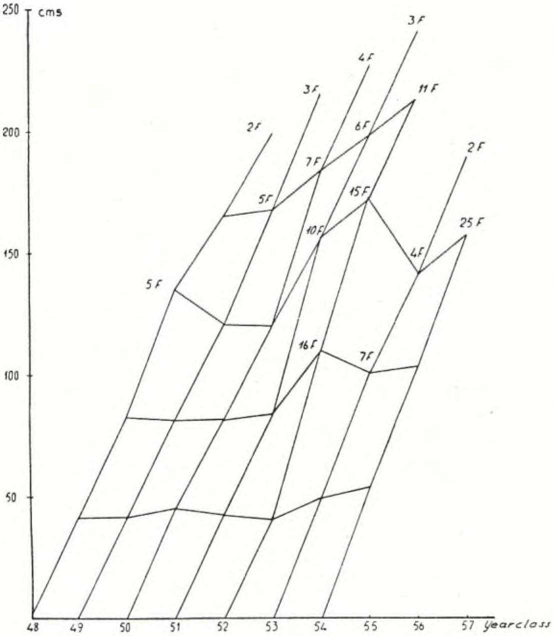

Fig. 31. Growth of different year classes of trout from the delta of Sannarån.

IV. Discussion

1. The invertebrate fauna of the delta before and after regulation

A comparison of the three closely examined plant biotopes in the delta of the Sannarån prior to the regulation (Tables I, II, and III) shows that the majority of the occurring genera are represented upon all examined plants. The quantity of the animals, however, differs for the different plant biotopes.

For the distribution of the animals in the vegetational belts the factor of nutrition seems to play an outstanding rôle. The epifauna is richest in the areas with *Myriophyllum alterniflorum* (Fig. 10), where also the representation of the epiphytes is most abundant. According to the foregoing many of the invertebrates found in the delta are herbivorous, and the carnivores, which found their prey among the former, have been attracted by their accumulation.

Upon *Carex vesicaria* (Fig. 8) the epiphytes are fewest, and also the epifauna is scantiest here. *Hirudinea, Acarina, Plecoptera,* and *Lamellibranchiata,* for instance, were not represented in the *Carex* belts.

With regard to the abundance of epifauna and epiphytes *Ranunculus peltatus* (Fig. 9) occupies a place intermediate between the two above-mentioned plants. Here, however, *Coleoptera* and *Lamellibranchiata* are missing.

Rehbronn (1937) has shown that aquatic plants with submerged filamentous leaves, e.g. *Myriophyllum,* in comparison with plants without submerged filamentous leaves, e.g. *Phragmites,* often carry among their epiflora an

Table VIII. Bottomsamples from the delta of River Sannarån 16—17th August 1954.

No Depth	XIII 12 m.			XIV 10 m.			XV 10 m.			XVI 8 m.		
10 × 2.25 dm²	Number of org.	Org. in % of all org.	Average org. per m²	Number of org.	Org. in % of all org.	Average org. per m²	Number of org.	Org. in % of all org.	Average org. per m²	Number of org.	Org. in % of all org.	Average org. per m²
Nematodes	21	28.4	93.3	43	21.2	191.1	61	17.9	271.1	—	—	—
Oligochaeta	—	—	—	111	54.7	493.3	—	—	—	396	88.0	1760.0
Helobdella stagn.	—	—	—	—	—	—	—	—	—	21	4.7	93.3
Daphnia long. hyal.	—	—	—	—	—	—	9	2.6	40.0	—	—	—
Cyclops sp.	—	—	—	—	—	—	11	3.2	48.9	—	—	—
Pentaneura	—	—	—	—	—	—	—	—	—	11	2.4	48.9
Sergentia sp.	53	71.6	235.6	17	8.4	75.6	260	76.2	1135.6	22	4.9	97.8
Chir. thummi	—	—	—	21	10.3	93.3	—	—	—	—	—	—
Gyraulis acr.	—	—	—	11	5.4	48.9	—	—	—	—	—	—
Sum	74	100.0	328.9	203	100.0	902.2	341	99.9	1515.6	450	100.0	2000.0

Table IX. Bottomsamples from the delta of River Sannarån 16—17th August 1954.

Depth: 3 m 10 × 2.25 dm²	August 16th 1954		
	Number of org.	Org. in % of all org.	Average org. per m²
Nematodes	53	7.4	764.5
Oligochaeta	250	34.8	1111.1
Eurycercus lam....	98	13.6	435.6
Polyphemus ped....	27	3.8	120.0
Pentaneura sp. ...	23	3.2	102.2
Sergentia sp.	187	26.0	831.1
Chir. thummi gr...	81	11.3	112.7
Sum	719	100.1	3477.2

additional layer of algae. Also *Ranunculus peltatus* can be counted among the plants with submerged filamentous leaves. It ought to be mentioned that *Ranunculus peltatus* grew in the most exposed place at the inlet of the delta (Fig. 3), that *Carex vesicaria* grew in more sheltered places, and *Myriophyllum alterniflorum* both in sheltered and exposed places. Samples from more sheltered places in the *Myriophyllum* belt contained more epiphytes than samples from more exposed places.

In the course of his investigation at Pellinge on the southern coast of Finland SEGERSTRÅLE (1927) found that the vegetation of *Fucus* contained fewer animals in more exposed than in sheltered spots. RAVERA (1951) showed that "the density fluctuations of benthonic organisms were directly or indirectly conditioned with the current velocity which varies largely in the different seasons". Since it is difficult to distinguish between the water current due to the wind in the delta and the current resulting from variations in drop, it is difficult to decide which of them exerts the greatest influence upon the distribution of the animals within the area. The *Myriophyllum* areas which were considered least exposed contained a greater amount of epifauna than those which had been deemed most exposed (Fig. 3). This is probably due to the point influence of food supply and degree of exposure.

The *Myriophyllum* belts in the delta of Sannarån formed, furthermore, denser carpets than the other vegetational belts, and this, in itself, reduces the exposition of the epifauna. *Myriophyllum alterniflorum* thus combined the two advantages of harbouring the greatest number of epiphytes and of offering the best hiding places. In the course of their investigations in Lake Mendota, Wisconsin, ANDREWS and HASLER (1944) found *Ceratophyllum demersum* and *Myriophyllum exalbescens to* contain the greatest number of animals per kg. of plant substances, viz. 52,000 and 29,000, respectively.

The distribution of the animals in the different plant biotopes proved to be subject to seasonal variation for which examples have been given in Chapter III. The variation is caused by the swarming of the animals, but also by other factors.

In America ROSINE (1955) has carried out investigations into the distribution of invertebrates upon sub-aquatic plants in Muskee Lake, Colorado. In this connection he found seasonal variation to exist for the epifauna upon *Chara, Polygonum,* and *Potamogeton.*

This circumstance is of great importance for the taking of the samples. Samples taken in a lake in June must not be compared without reservation with samples taken, e.g., in August in another lake, unless a basic idea has been previously obtained about the biological phenomena in the lakes in question. Many examples of such mistakes can, however, be found in the literature.

The occurrence per sq.m. of *Ranunculus peltatus* from June to August

Table X. Food of trout and char catched in the delta of River Sannarån June—August 1949 and July 1957.

Species and date	Number of fish	Oligochaeta		Hirudinea		Eurycercus		Polyphemus		Heterocope		Gammarus		Hydracarina		Plecoptera l.		Ephemeroptera l.		Ephemeroptera i.		Neuroptera (Sialidae)		Trichoptera l.		Trichoptera p.i.		Chironomidae l.		Chironomidae i.		Culicidae l.		Culicidae i.		Simulidae i.		Tipulidae l.		Carabidae i.		Dytiscidae l.		Dytiscidae i.		Staphylinidae i.		Cantharidae i.		Cerambycidae (callidium)		Formicidae		Hemiptera		Gastropoda		Unidentified rests	Organisms totally		Min. and max. length of the catched fishes
		N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V	N	V	V	N	V	
Trout																																																													
20/6-49	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12	0.15	63	0.63	—	—	—	—	10	0.67	—	—	22	0.06	—	—	—	—	—	—	42	0.32	—	—	—	—	1	0.02	1	0.02	—	—	—	—	—	—	—	—	—	—	—	—	0.41	151	1.9	27—33
28/6-49	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9	0.11	34	0.43	—	—	—	—	9	0.51	—	—	7	0.03	—	—	—	—	—	—	47	0.45	—	—	—	—					—	—	—	—	—	—	—	—	—	—	—	—	0.70	106	1.5	17—33
June Sum..............	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	21	0.26	97	1.06	—	—	—	—	19	1.18	—	—	29	0.09	—	—	—	—	—	—	89	0.77	—	—	—	—	1	0.02	1	0.02	—	—	—	—	—	—	—	—	—	—	—	—	1.11	257	3.4	—
Percent of volume: sum...	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5.8	—	23.6	—	—	—	—	—	26.1	—	—	—	2.0	—	—	—	—	—	—	.—	17.1	—	—	—	—	—	0.4	—	0.4	—	—	—	—	—	—	—	—	—	—	—	—	24.6	Sum	100.0	—
Trout																																																												
8/7-49	23	—	—	—	—	—	—	—	—	—	—	14	1.0	26	0.07	25	11.4	462	6.02	—	—	6	0.4	203	11.3	61	3.9	316	0.75	—	—	—	—	—	—	106	10.2	—	—	—	—	4	0.2	1	0.1	1	0.1	—	—	—	—	—	—	—	—	—	—	14.7	1225	45.4	16—31
12/7-49	16	—	—	—	—	1	0.01	—	—	—	—	105	2.2	—	—	—	—	8	0.4	—	—	—	—	75	3.5	1	0.2	641	1.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	0.1	—	—	—	—	—	—	—	—	—	—	15.1	832	7.5	15—31
19/7-49	28	3	0.2	—	—	20	0.1	—	—	—	—	34	2.9	—	—	2	0.09	122	4.8	2	0.1	—	—	175	8.6	19	2.1	369	1.3	8	0.9	—	—	—	—	94	1.7	1	0.2	—	—	4	0.7	4	0.3	—	—	—	—	5	0.3	—	—	—	—	1	0.1	27.4	863	24.4	14—32
22/7-49	14	—	—	—	—	—	—	—	—	—	—	1	0.1	—	—	—	—	13	0.3	—	—	—	—	69	3.3	11	1.2	5	0.03	8	0.04	—	—	—	—	6	0.11	—	—	4	0.3	—	—	13	1.8	—	—	5	0.5	—	—	—	—	1	0.1	4	0.3	11.0	140	8.1	17—32
27/7-49	19	6	0.5	—	—	28	0.1	—	—	—	—	2	0.1	1	0.02	—	—	146	1.8	—	—	—	—	84	4.7	2	0.1	16	0.13	—	—	—	—	—	—	45	0.2	—	—	7	1.12	7	0.4	—	—	—	—	—	—	—	—	1	0.2	—	—	—	—	61.5	345	9.4	14--34
July Sum..............	100	9	0.7	—	—	49	0.21	—	—	—	—	156	6.3	27	0.09	27	11.49	751	13.32	2	0.1	6	0.4	606	31.4	94	7.5	1347	3.31	16	0.94	—	—	—	—	251	12.21	1	0.2	11	1.42	15	1.3	18	2.2	2	0.2	5	0.5	5	0.3	1	0.2	1	0.1	5	0.4	129.7	3405	94.8	—
Percent of volyme: Sum...	—	—	0.3	—	—	—	0.1	—	—	—	—	—	2.8	—	0.1	—	5.1	—	6.0	—	0.1	—	0.2	—	14.0	—	3.4	—	1.5	—	0.4	—	—	—	—	—	5.4	—	0.1	—	0.6	—	0.6	—	1.0	—	0.1	—	0.2	—	0.1	—	0.1	—	0.1	—	0.2	57.5	Sum	100.0	—
Trout																																																												
2/8-49	14	—	—	—	—	5	0.02	—	—	—	—	2	0.3	—	—	—	—	95	1.7	—	—	—	—	30	0.9	30	1.0	98	0.3	1	0.01	—	—	—	—	13	0.5	—	—	—	—	5	0.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7.5	279	4.8	12—33
6/8-49	14	5	0.6	1	0.1	—	—	—	—	—	—	2	0.1	—	—	—	—	49	3.5	6	0.5	—	—	16	0.9	13	1.7	10	0.07	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	0.1	—	—	—	—	11.5	107	7.6	20--40
9/8-49	24	—	—	—	—	—	—	—	—	—	—	1	0.1	—	—	1	0.3	50	1.3	—	—	5	0.3	63	2.3	53	5.0	27	0.1	—	—	—	—	—	—	6	0.2	—	—	—	—	31	1.0	4	0.4	—	—	—	—	—	—	—	—	—	—	—	—	10.1	241	11.0	17—36
16/8-49	12	—	—	—	—	—	—	—	—	—	—			—	—	—	—	33	0.8	—	—	—	—	14	0.5	67	3.3	7	0.02	153	0.4	—	—	—	—	8	0.2	—	—	—	—	2	0.1	—	—	—	—	—	—	2	0.1	—	—	—	—	—	—	1.9	286	5.4	14—23
23/8-49	28	—	—	—	—	105	0.3	—	—	—	—	3	0.6	—	—	3	0.15	164	1.7	—	—	—	—	99	2.7	179	9.5	19	0.05	—	—	2	0.1	3	0.1	20	0.5	—	—	—	—	31	1.1	—	—	—	—	—	—	—	—	1	0.01	—	—	9	0.6	15.7	638	17.4	9—28
26/8-49	8	—	—	—	—	—	—	—	—	—	—	49	0.8	—	—	—	—	—	—	—	—	—	—	1	0.1	—	—	6	0.05	—	—	—	—	—	—	—	—	—	—	—	—	1	0.1	—	—	2	0.2	—	—	—	—	34	0.9	—	—	—	—	3.6	93	2.2	17—46
August Sum..............	100	5	0.6	1	0.1	110	0.32	—	—	—	—	57	1.9	—	—	4	0.45	391	9.0	6	0.5	5	0.3	223	7.4	342	20.5	167	0.59	154	0.41	2	0.1	3	0.1	47	1.4	—	—	—	—	70	2.4	4	0.4	2	0.2	—	—	2	0.1	40	1.01	—	—	9	0.6	50.3	1644	48.4	—
Percent of volume: Sum...	—	—	0.6	—	0.1	—	0.3	—	—	—	—	—	2.0	—	—	—	0.5	—	9.1	—	0.5	—	0.3	—	7.5	—	20.8	—	0.6	—	0.4	—	0.1	—	0.1	—	1.5	—	—	—	—	—	2.4	—	0.4	—	0.2	—	—	—	0.1		1.0	—	—	—	0.6	50.9	Sum	100.0	—
Trout 1957 25/7—26/7	37	44	0.94	5	0.24	352	0.44	—	—	—	—	—	—	—	—	5	0.15	452	4.47	—	—	—	—	12	0.45	49	2.55	466	0.94	12	0.19	—	—	—	—	51	0.30	—	—	—	—	13	0.20	19	0.64	—	—	—	—	—	—	—	—	—	—	—	—	5.6	1480	11.5	14.5—27.5
July Sum..............	37	44	0.94	5	0.24	352	0.44	—	—	—	—	—	—	—	—	5	0.15	452	4.47	—	—	—	—	12	0.45	49	2.55	466	0.94	12	0.19	—	—	—	—	51	0.30	—	—	—	—	13	0.20	19	0.64	—	—	—	—	—	—	—	—	—	—	—	—	5.6	1480	11.5	—
Percent of volume: Sum...	—	—	5.5	—	1.3	—	2.6	—	—	—	—	—	—	—	—	—	0.8	—	26.3	—	—	—	—	—	2.6	—	15.0	—	5.5	—	1.1	—	—	—	—	—	1.6	—	—	—	—	—	1.2	—	3.8	—	—	—	—	—	—	—	—	—	—	—	—	32.7	Sum	100.0	—
Char 1957 25/7—26/7	37	26	0.59	—	—	2403	1.98	18	0.05	82	0.08	—	—	—	—	12	0.09	231	0.93	—	—	—	—	31	0.12	6	0.1	2424	2.63	17	0.22	—	—	—	—	—	—	—	—	—	—	—	—	2	0.04	—	—	—	—	—	—	—	—	—	—	—	—	3.4	5252	6.8	14.5—26.0
July Sum..............	37	26	0.59	—	—	2403	1.98	18	0.05	82	0.08	—	—	—	—	12	0.09	231	0.93	—	—	—	—	31	0.12	6	0.1	2424	2.63	17	0.22	—	—	—	—	—	—	—	—	—	—	—	—	2	0.04	—	—	—	—	—	—	—	—	—	—	—	—	3.4	5252	6.8	—
Percent of volume: Sum...	—	—	5.8	—	—	—	19.4	—	0.5	—	0.8	—	—	—	—	—	0.9	—	9.1	—	—	—	—	—	1.2	—	1.0	—	25.8	—	2.2	—	—	—	—	—	—	—	—	—	—	—	—	—	0.4	—	—	—	—	—	—	—	—	—	—	—	—	32.9	Sum	100.0	—

increased more than that of the other macrophytes treated. In addition, the vertical distribution in the basin of *Ranunculus peltatus* was greater than that of the other discussed plants (Fig. 4). *Carex vesicaria* differed from the other plants by the partial exposure of the plant above the surface of the water. These features of *Ranunculus* and *Carex,* respectively, exert a corresponding influence upon the distribution of the epifauna.

In summing up we can state that the variation in the distribution of the animals over the different plant biotopes can arise, amongst others, from

1) variation in the supply of food for the herbivores,
2) increase or decrease of the populations of animals preyed upon at inverse ratio to the numbers of their enemies,
3) changes in the degree of exposure,
4) swarming, and
5) natural death.

In 1949 the naked bottoms (Table IV), in the delta of Sannarån proved to contain a much smaller number of species than those covered with vegetation. By their ratio number/sq.m. the oligochaetes dominated during all months of the investigation with the exception of June, when *Polyphemus* formed the largest group of animals, followed next by the oligochaetes. In Chapter III: 3 a it has been pointed out that *Polyphemus* is a planktonic animal which forms clusters, and that its dominance in the samples from June might be coincidently. Upon the naked bottoms the insects were represented by the chironomids only.

There exist also samples from the naked bottoms from 1948 (Table IV). A comparison of the samples for August of 1948 and 1949, respectively, shows that besides variation between the months, which has already been discussed (see the whole Table IV), there is also a variation between years. The total number of organisms per sq.m. in August was larger in 1949 than in 1948. The percentage in the entire fauna of the oligochaetes in August 1949 was about twice as large as in August 1948. According to information from SMHI (The Meteorological and Hydrological Institute of Sweden) 1948—1957 the precipitation in the drainage area of Borgafjäll for the time August 1—15 was 22.6 mms. in 1948, and 58.9 mms. in 1949. Since it is probable that the richer precipitation in August 1949 has resulted in a greater amount of water in the brooks, and thereby in a richer sedimentation in the region of the lake, it is conceivable that in 1949 the food supply for the oligochaetes was more abundant than in 1948.

In the delta of Sannarån we have observed how a great number of animals are strongly linked to the aquatic vegetation, and that also under normal conditions fairly great variations in the mutual distribution of the species could arise both in the vegetation and upon naked bottoms.

The delta of Sannarån was situated in fairly flat country, with the result that with the regulation its surroundings was overflooded, and that the dammed-up surface of water is much larger than the original. The fluctuations of the water-level before and after the regulation can be seen in Fig. 27.

The course of a biological phenomenon is in most cases determined not by a single factor, a key factor, but by a multitude of factors, especially in the case of such a profound interference with natural conditions as the regulation of a lake. In the delta of Sannarån the changes became particularly great, since the damming-up transformed the river connecting Borgasjön and the lake Sannaren (Fig. 1) into a lake which also includes the delta.

Samples taken in August 1954, i.e. in the third year of the damming-up of the delta of Sannarån showed that the former vegetational belts in the delta had been completely destroyed, as had also been expected.

The increased depth of the water in the delta of Sannarån, which in 1954 was about thrice that of 1949, and the decreasing penetration of the sunlight, made more difficult also by the turbidity of the water caused by the erosion of loose soils in the overflooded areas, — the depth of sight in 1949 being 1 m. greater than in 1954 —, were factors caused by the damming. QUENNERSTEDT (1955) who carried out an investigation into the effect of the regulation of lakes upon the vegetation in lakes of Jämtland found that the changes of water-level destroy the original vegetation in the lakes, since a rise of the waterlevel of sufficient durability and order of magnitude excluded the possibilities of existence for all perennial plants and for all other organisms that for their occurrence are dependent on these plants.

A comparison of the fauna before (Table I, II, III, and IV, and Figs. 8—10) and after the regulation (Tables V—X) shows, how the damming-up has influenced the fauna in the delta. The most obvious difference seems to be the intense change in the insect fauna which in 1949 was linked with the plant biotopes. In 1954 a great part of the fauna (*Acarina, Plecoptera, Ephemeroptera, Neuroptera, Coleoptera,* and the majority of the *Trichoptera*) had completely disappeared from the delta. Neither has it been possible to rediscover the disappeared part of the fauna in a sample taken in 1954 outside the delta in a depth of three metres (Table IX).

Among the animals which resisted the damming-up very well are noticed the oligochaetes, since in most samples of 1954 they form the major part of the animals. The samples of 1949 (Table IV) show in August, and at the depth of 1 m. a maximum of oligochaetes amounting to 2,177 organisms per square metre. At the depth of 8 metres the samples gave for 1954 (Table V: II) a maximum of 3,795 organisms per spuare metre.

In the upper littoral of Lake Innaren BRUNDIN (1949) found for the oligochaetes a maximum density of 5,070 ind./sq.m. At a depth of 12—13 metres he found 174 ind./sq.m. and at 14—15 metres 285 ind./sq.m., and pronounced this as comparatively high. On this basis the fauna of the oligochaetes in the delta of Sannarån after the regulation can be considered as very abundant, since it has shifted deeper down. The great number of oligochaetes probably depends to a large extent on contributions from the soil washed down from the cultivations in the immediate vicinity of the former delta. This soil has been mixed up with mouldering plant substance, etc., and has thereby formed a biotope which is favourable just for oligochaetes. A study of the different samples in Tables V—IX shows the fauna of the oligochaetes to be very unevenly distributed over the sampling area, certainly on account of the heterogeneity of the sedimentation. Already before the regulation of the lake differences of the bottom sediments both in hardness and in grain size on the detached sediment were observed when the samples were taken. In the course of his examination of the delta in the river Toce RAVERA (1951) established within the delta great ecological differences which also brought about great differences, qualitative as well as quantitative, within the benthonic colonies. In RAVERA's samples the tubificids formed the most important component. These he proved to be richly represented where the sediments contain a high percentage of organic substances. This constitutes perhaps one of the explanations which can be offered for the uneven distribution of the oligochaete fauna after the regulation upon the bottoms within the delta of Sannarån.

After the regulation of the lake the vagile nematodes occupy an important place in the samples (Tables V—IX). The nematodes are omnivorous, and play a great part in the decomposition of organic substance (MENZEL 1920). Their eggs are very resistant to, amongst others, lengthy deficiency of oxygen and freezing-in (PENNAK 1953, p. 220). This permits the conclusion that they have a good chance of surviving a regulation of a lake. In the samples from 1949 no nematodes were found. Probably they have spread in connection with the regulation from those areas, where they are otherwise found. They might also have been so small in 1949 that they then were lost through the selective action of the straining-cloth.

If we restrict comparison to the samples taken in August upon sedimentary bottoms before and after a rise of the water-level in the delta, we obtain an increase of the stock of *Eurycercus* though in patches. A comparison in August of the delta of Sannarån as a whole before and after the regulation of the lake results on the other hand in a decrease.

DAHL (1926), who in Norway carried out investigations of the regulated Tunhövdfjord, found during August, i.e. one year after the first damming, an enormous amount of *Entomostraca* (*Eurycercus* and *Sida chrystallina*) at depths from 0 to 2 metres. Three years later, however, the number of *Entomostraca* at 0—3 ms. was smaller. In sampling DAHL used EKMAN's bottom grab before, and mainly the netting method after the regulation of the fjord, and is therefore unable to supply any exact quantitative information. His results point nevertheless in the direction towards an increase in the occurrence of the semi-floating, semi-planktonic *Crustacea.*

During his studies in the water storage basin in Gudbrandsdalen OLSTAD (1925) observed that under normal conditions *Eurycercus lamellatus* occurs most numerously in connection with submersed vegetation (cf. also WEIGOLD 1914), but that it occured during highwater, when also dry land was inundated for a longer time, in great numbers at overgrown bottoms and was missing or rare upon bottoms without vegetation. The decrease of the stock of *Eurycercus* which in accordance with the foregoing was shown in the delta of Sannarån after the regulation as a consequence of the disappearance of the submersed macrophytes agrees with OLSTAD's observations.

Thus there is some uncertainty how to explain DAHL's observations. It is obvious that both the abundance of Eurycercus in the macrophytes and over the naked bottoms should be studied when investigating lake regulations.

Gammarus was not rediscovered in the samples from the delta of 1954, neither was it found outside the delta at the depth of 3 metres (Tables V—IX). This entirely agrees with the results obtained by DAHL (1926) who did not find *Gammarus* after the damming-up of Tunhövdfjord.

For *Gammarus lacustris* it is of importance that there exist during the time of propagation good hiding places for moulting, etc. In order to understand the abscence of *Gammarus* from the samples from the delta of 1954 it is certainly of importance to keep in mind the changes which have been introduced by the loss of the good hiding places and hunting grounds, supplied previously by the vegetational belts, and to remember that sexual maturity is reached only after about 2 years. When the water froze the animals have developed visible ovaries, and have in the shallow water become an easy prey for fishes.

Also of *Hydracarina, Plecoptera, Ephemeroptera,* and *Neuroptera* no rediscoveries have been made in August 1954.

According to LUNDBLAD (1927) the *Hydracarina* exhibit a pronounced predilection for rich vegetation. This being absent in the delta of Sannarån 1954, the biotope of these animals was spoilt.

As the *Plecoptera* which occurred in the delta of Sannarån seemed to swarm in August, it is difficult to draw any conclusions from their absence in August 1954. With regard to *Plecoptera* BRINCK (1949, p. 182) points out that "the seasonal variations of the flow may be very important and highly affects the composition of the stone-fly fauna when approaching minimum values".

After the filling of the storage basin the delta of Sannarån assumes the characteristics of a lake. With reference to BRINCK's results this can also with certainty be taken as having influenced the composition of the fauna of *Plecoptera* in the delta. The species of *Plecoptera* which live in running water are quite naturally especially vulnerable, when the biotope is transformed into a lake. "*Nemouridae* all feed on higher plant and moss tissues" (BRINCK 1949, p. 156). Therefore also lack of suitable food might have been of influence.

In 1938 LINDUSKA (1942) studied the distribution of the larvae of ephemerids upon different types of bottom in Rattlesnake Creek, Montana. He found that the larvae of ephemerids 1) occur in the greatest concentrations in well defined types of stream bottom, 2) are dependent to such an extent on certain substrata so well defined as to exclude them from portions of the stream lacking in given bottom types. 3) The velocity of the current as such had no visible influence upon the limitation of the local distribution in places, where acceptable bottom types occurred. 4) Within a given site, stream flow appeared responsible for a vertical distribution of nymphs, due presumably to the different abilities of species to withstand current. The species of Ephemeroptera in the delta of Sannarån were strongly associated with the macrophyte biotope. None of the detected species belonged to the burrowing species. Their biotope had been changed totally after regulation, when the macrophytes had been destroyed and according to LINDUSKA the mayflies must disappear which also was confirmed by the investigations in 1954.

The reduction between August 1949 and August 1954 of the number of genera of *Trichoptera* from one to five is remarkable. Most of the other genera of *Trichoptera* which were represented in July 1949 seemed to swarm in August. This can explain the small number of genera in August 1954. Since, however, the diet of the fish, which has been examined in 1957, and which will be discussed in a later chapter, is going to corroborate the decline of the *Trichoptera,* we can conclude also here that also the chances of survival of the *Trichoptera* have been reduced.

In 1954 the *Trichoptera* are represented only by some few *Limnophiles sp.* with sand cases in sample III from 8 ms.' depth (Table V). This group of animals was not found in any of the samples from August 1949, neither upon overgrown nor upon naked bottoms, but well during July upon *Myriophyllum alterniflorum* and *Carex vesicaria,* preponderately upon the latter with cases built of fragments of plants. Of the *Limnophilidae* some swarm early, some late (ULMER 1909). The material for the building of the cases seems generally not to be an ecological factor which determines the linking of the species to a certain biotope, as one might be tempted to believe from the similarities of the material for the building of the cases found within one and the same species. An exception has to be made for strong currents, where weight and shape of the material are of importance (DODDS and HISAW 1924). *Limnophilus* is either represented by different species in 1949 and 1954, or the same species has changed the material from which it builds its cases. On the basis of the available material this question cannot be answered.

Swimming larvae are rare among *Trichoptera* (DODDS and HISAW 1925). The pupa, on the other hand, moves by swift swimming, but is unable to cover longer distances. (WESENBERG-LUND 1943). This feeble ability of locomotion may have contributed to the difficulties experienced by the *Trichoptera* to adapt themselves to the new biotope in 1954, when the depth had considerably increased.

In the course of their studies of different species of *Trichoptera* in the Colorado Rockies DODDS and HISAW (1925) found that for the existence of certain species swift running water was a necessity. Also *Hydropsychidae* and *Polycentropidae* which are netspinning, and as a rule live in running water, had disappeared from the delta in 1954, since the now increasingly lake-like character of the delta had completely changed their biotope.

Among the *Diptera* the chironomids seem to have endured the regulation of the lake relatively well (Tables IV—IX). A remarkable fact is the great expansion of *Sergentia sp.* which before the regulation was not represented in the examined epifauna, yet by a small number of specimens in the bottom samples of 1949 (Table IV). *Microtendipes sp.* which in 1954 was represented by 53.3 organisms per square metre, was not found in 1949 in any of the samples from the delta. It occurred, however, in a mixed belt of *Sparganium* and *Potamogeton* outside the delta (manuscript note in the Institute for Freshwater Research).

We have established that many chironomids and oligochaetes have supported the regulation of the lake well. Some data from ALSTERBERG's paper (1925) will show that the biotope of these groups of animals has remained favourable also after the regulation of the lake. ALSTERBERG established that the tubificids, like the lumbricids, transport material from below upwards. In the deeper layers of the mud they dug upwardly directed passages of irregular width. In the following layer they formed narrow vertical passages in which the animals could move the posterior part of the body forwards and backwards. This layer was situated at a depth of 3—6 cms., counted from the surface of the mud. Between these two layers existed a limiting layer, the nutritive layer, in which the anterior part of the animal was anchored. The excrements were always deposited in the uppermost layer. The nutritive layer is invariably fixed to a certain level, and the movements of the animals are always carried out in such a way that they remain in this layer.

In the same paper ALSTERBERG also deals with the life at the bottom of certain chironomids. In general the chironomids did not work in the mud deeper than 2 cms. Contrary to the tubificids they contributed to the aeration of the mud. The group of *Tanypus* did not consume any mud at all, but lived on certain green algae, diatoms, and even tubificids.

The *Chironomus*-group on the other hand consumed mud, and it was proved that they simply could not digest living material. The nutritive layer of the chironomids was, however, situated in the upper part of the layer of mud. Thus tubificids and chironomids live in different niches. According to the above they collaborate in the aeration of the layer of mud, and effect a faster filtration of the mud as if each group of animals would work by itself. Also in the case of pollution of the water oligochaetes and chironomids have been found to increase in numbers.

Also the oxygen and temperature factor are of great influence. ALSTERBERG (1922) has proved that mud which contains practically no oxygen, but is on the other hand rich in reducing substances consumes the oxygen store of the water at the bottom with the result that water poor in oxygen lies directly above the mud. We thus find a kind of micro-stratification in the lowermost part of the water at the bottom. After the regulation of a lake, when the mud of the bottom has been mixed up with a great amount of organic particles (the smell of hydrogen sulphide from the mud of the bottom of the delta of Sannarån could be felt in 1954) a consumption of oxygen ought to take place, and a microstratification like the above observed by ALSTERBERG could possibly be formed. In this case complications can arise for bottom animals that are unable to exist with a small store of oxygen. *Prodiamesa,* which was not rediscovered in 1954 in the delta of Sannarån, belongs to the chironomids which require a fair amount of oxygen.

BRUNDIN (1951) has established that a deficiency of oxygen at the bottom is unfavourable especially for the small larvae of chironomids, e.g. of the *Tanytarsus*-group (absent from the delta in 1954), but does not affect the larger larvae of *Stichtochironomus* and *Sergentia* in any degree worth mentioning. In the above we have seen that is was just *Sergentia* and the group of *Chironomus thummi* which among the chironomids occurred also after the damming.

Coleoptera which before the damming-up were represented only by *Dytiscus marginalis* (*Dytiscidae*) were not rediscovered in the samples from the delta of 1954. They were, however, very scarce already before the regulation of the lake.

According to WESENBERG-LUND (1943) *Dytiscus marginalis* is dependent on plants for the deposition of its eggs. For this reason the disappearance of the former vegetational belts has considerably reduced its chances of finding suitable biotope in the delta of Sannarån.

Among the *Gastropoda Gyraulis acronicus* was rediscovered in samples from the depth of 10 ms. taken in August 1954 (Table VIII: XIV). The two other species which had been found in 1949 in the delta om Sannarån (Tables I—III) came from samples taken in June and July. In August 1954 the two species of gastropods were not rediscovered in the samples. Since, however, no samples have been taken in June and July of this year, it is not possible to assert that they have disappeared on account of the regulation. DAHL (1926) observed in Tunhövdfjord a diminution of snails. This apparently agrees with my results, but also DAHL's observations can not be considered conclusive, as he compares samples from July before the regulation with such from August after the regulation.

Among the animals which according to DAHL suffered least in the Tunhövdfjord were the pisidiids. In the delta of Sannarån *Pisidium sp.* was rediscovered in a depth of 8 ms. in a number of 182.2 per square metre (Table V: II). Before the damming *Pisidium* occurred only in the *Myriophyllum* belt, and there in August (Table II) in a number of 9 individuals per 1 kg. of plant substance, or, after recalculation, about 31 individuals per sq.m. This would indicate an increase after the damming. Acording to verbal information received from Prof. N. ODHNER there exist two forms, viz. pisidiids of the deep water which reproduce themselves throughout the year, and pisidiids of the shallow water which reproduce themselves only in the warmest season. According to ODHNER (1951) the pisidiids are not linked in general to a definite biotope, and are easily spread, e.g. by birds. After the damming-up the delta of Sannarån seems, however, most suited for the deep-water form among the pisidiids. On the whole we can observe that the regulation has favoured the fauna of pisidiids.

The most outstanding characters of the fauna of the delta of Sannarån prior to the damming-up were 1) that is was composed of a mixture of forms living in running water, and of forms which were more adapted to life in lakes, with a strong linkage to the vegetational biotopes. 2) Among the most outstanding groups of animals (Figs. 8—10) were noticed *Phyllopoda, Ephemeroptera, Oligochaeta, Diptera,* and *Trichoptera.* 3) Its standing crop varied with the substratum, the bottoms covered with vegetation being much richer both quantitatively and qualitatively than the naked bottoms.

When after the damming-up the delta had assumed more lakelike features, and was situated at greater depth the most noticeable differences consist in 1) a decided decrease in the number of types of organisms, 2) a shifting of the dominance towards *Oligochaeta, Diptera,* and *Nematoda,* and 3) a quantitative difference in the standing crop with a decrease upon the formerly vegetational bottoms and an increase after the damming-up upon the former so-called naked bottoms.

My investigations in the delta of Sannarån have produced results that agree with those obtained by CHAMPBELL and O'CONNEL jr. (1953) in the Black River- and Clearwater Lake of Missouri. There the damming-up was effected in such a way that a dam was built in a part of the Black River for the purpose of flood control. There the fauna was considerably richer than in the delta of Sannarån, but was much impoverished after the damming as far as types of organisms are concerned. Also here the macrophytes disappeared with the rising of the overflow threshold.

2. Availability of food and the feeding habits of fish in the delta of River Sannarån before and after regulation

As far as I know no investigations into the food habits of the trout have previously been carried out in Sweden in connection with a simultaneous examination of the epifauna.

a. Before regulation.

In 1949 the delta of Sannarån was found to be an appreciated dwelling place of growing trout most of which belonged to the age groups of 3—4 years. These had certainly been attracted to the delta by the good hiding places and by the accumulation of prey afforded in the vegetational belts. They probably fed in the places of their capture. Literature admittedly contains information about periodic distant migrations of the trout (ARVIDSSON 1935, SØMME 1941, and others), but in connection with the fishing the delta was closed in with nets to the greatest possible extent (Chapter III: 4). To this can be added the indications of the fish being periodically stationary in the delta which can be gathered from the result of the marking experiments, since of 23 fishes which had been liberated in the delta three were recovered in the delta in the following year. Neither is it probable that the stomach content would agree so well with the fauna of the delta as we shall show in the following, if the food were derived from a fauna of different composition.

The samples of stomachs which have been examined in the delta of Sannarån in 1949 supplied a fairly good picture of the conditions existing in the delta. The seasonal variation which in the foregoing has been established for the animals serving as food were reproduced also in the samples of stomachs. From the Figs. 28—30 can be seen that in June *Ephemeroptera.* l. dominate in numbers. They are succeeded by *Simulidae* i., *Chironomidae* l., *Plecoptera* l., and *Trichoptera* l.

During July *Chironomidae* l. dominate in numbers, being followed by *Ephemeroptera* l., *Trichoptera* l., *Simulidae* i., *Gammarus, Trichoptera* i., and *Eurycercus,* in this order.

During August *Ephemeroptera* l. have risen to the first place, being followed in order of numbers by *Trichoptera* i., *Chironomidae* l. and i., respectively, *Eurycercus, Dytiscidae* l. *Gammarus, Simulidae* i., and *Formicidae*. Surface food seems to be more important in August than in July.

With a point of view of deciding whether or not the variation in the diet of the fishes was linked more particularly to variation of the surrounding epifauna comparisons were carried out for each group of animals between the stomach content (Tab. XI; Figs. 28—30) and the epifauna (Tab. I—III; Figs. 8—10). In order to facilitate a general survey of these conditions a compilation of the results of these comparisons has been given in Tab. XI, where E=epifauna, M=stomach content, and where the sign "+" designates the month with the highest number in epifauna and the month with the highest number in the stomach contents. Comparison are only made within a group of animal. June has been excluded from the comparison, the number of fishes caught in this month being too small. The synoptical Table XI shows that on the whole the fishes seem to consume most of the prey which is most richly represented in the epifauna. This is illustrated e.g. by the fact that in July (Fig. 11) the oligochaetes are more abundant in number/kg of plant substance than in August, and that in August *Eurycercus* Fig. 13 is better represented in the epifauna than in July, and that this variation finds its exact conterpart in the diet of the fishes. There exists thus a similarity between epifauna and diet of fishes. All animals eaten by the fish could in some way be connected with the fauna in the delta of Sannarån. If, for instance, the occurrence of *Chironomidae* l. in the epifauna was feeble in one of the compared months in relation to the other, the hatching time for the group of animals was calculated. This could then be corroborated by the comparison of the stomach samples which in relation to the larvae contained a greater number of imagines. A great number of terrestrial animals corresponds to an abundant supply of such in the delta of Sannarån. It is a well known fact that abundance of *Geometridae* is found in the stomach samples in years, when great numbers of these animals drop into the water. They can have been carried into the water by a favourable wind, by rain, or in any other way, and can thereby have become more easily accessible to the fish.

The undigested remains are, however, largest in July, when also a greater amount of chitinous food (*Coleoptera* i.) is consumed than in August.

In spite of the good agreement between the available food and the consumption there exist nevertheless minor divergences indicative of a selection, since not all the animals of the fauna were represented in the stomach of the fishes. This can be imagined to depend upon the fact that some animals were rare, not easily accessible on account of their mode of life, difficult to catch on account of the swiftness of movement, too small or too large for serving as food, etc.

Gammarus, e.g., occurs in the stomach of the fish more in July than in August, in spite of the fact that its frequency in the epifauna shows the opposite picture. The gammarids which were represented in the epifauna of July were in general adult females, that had recently dropped their young from the marsupium, and females that still carried young. The total number of *Gammarus* for July was 23.7 specimens per kg of plant substance, and for August 36.3 specimens per kg. As a large number of the gammarids caught in July was females that had newly delivered their brood, it seems possible that these animals more easily caught, since after the liberation of the brood the condition of the females ought to be somewhat enfeebled.

Table XI.

	Myriophyllum			
	July		August	
	E $\left(\frac{A}{K}\right)$	M (ΣN)	E	M
Oligochaeta	148.4 +	9 +	29.1	5
Hirudinea	25.4 +	—	24.8	1 +
Eurycercus	148.0	49	304.2 +	110 +
Gammarus	16.8	156 +	33.9 +	57
Hydracarina	10.1 +	27 +	6.35	—
Plecoptera l.	6.97 +	27 +	1.08	4
Ephemeroptera l. ..	106.3 +	751 +	76.6	391
Neuroptera (Sialidae)	1.0 +	6 +	—	5
Trichoptera l.	20.2 +	606 +	14.6	223
Chironomidae l.	120.0 +	1347 +	56.7	167
Dytiscidae l.	—	15	2.0 +	70 +
Gastropoda	8.2	5	31.5 +	9 +

Large animals are furthermore better visible than smaller ones, unless they have a protective colouration in relation to the surroundings.

A comparison of epifauna and sedimentary bottom fauna on the basis of the density per square metre according to Chapter IV: 1 is perhaps less suitable, the epifauna being more spread in space. It proved, however, the epifauna to be richer than the bottom fauna. Also the food of the fish showed a dominance of the epifauna compared with the bottom fauna. The feeding fish thus does not feed the same length of time in every place, but remains longer in the vegetational areas than upon the naked bottoms, attracted probably by the density of the epifauna according to the foregoing and by the suitable hiding places which can be available there. This is corroborated by the fishing records, the catch per net being greatest in the vegetational areas. The place, where the fish has caught the surface food and their density upon the surface of the water, are not known.

HESS and SWARTZ (1941), ALLEN (1941, 1942, 1951), and others have discussed the choice by the fish among the food available in the environment, and have calculated an "availability factor" or "forage ratio" expressing the relation between fauna and food. The most important result in the delta of Sannarån is the good agreement between the surrounding fauna and the choice of food of the fish.

b. After regulation.

During the first time after the damming-up the fish seemed to shun the former delta as far as can be judged from the fishing records, (kept in manuscript in the Institute for Freshwater Research). In spite of the intensive fishing in the former delta in connection with the bottom sampling carried out in 1954 no trout were obtained, only a few chars and burbots.

In connection with earlier investigations of regulated lakes (RUNNSTRÖM 1951, 1952) the fish was found to move to the newly flooded bottoms, where more abundant food was available.

The same result had previously been obtained in the course of examinations of damming enterprises abroad (DAHL 1926, HUITFELDT-KAAS 1935, MARTIN and CAMPBELL 1953, CAMPBELL 1954). On this account it is most likely that the absence during the first time of the fish in the delta of Sannarån is due to the same reasons. It is also conceivable that the turbidity of the water due to erosion, which expressed itself in 1954 by feebler transparency of the water as compared with 1949, could in some measure contribute in driving the fish away from the delta. On this account we possess from 1954 no stomach samples from the former delta, but only bottom samples.

In 1957, five years after the damming-up, the conditions were different. Now the former delta was invaded by char. The trout, however, stayed in shallower areas outside the delta. In this year no bottom samples were taken, but only stomach samples, preventing direct comparisons with the surrounding fauna. Under these circumstances we assume as the best hypothesis that the fauna of the delta has changed only little between 1954 and 1957. With regard to the submerged fauna on the impounded area such a hypothesis can not be expressed without certain reservations.

In the year 1957 it appears less certain that the fish have caught their food in the places of capture, than it was 1949 but according to the foregoing a distribution of char and trout in deep and shallow water, respectively, could be observed. It is possible also to demonstrate a certain agreement between the composition of food of the fish and the bottom samples of 1954. Table X shows that, volumetrically, the trout consumed mainly larvae of ephemerids (mainly *Siphlonurus sp.*) (26.3 %, then imagines of *Trichoptera* (15.0 %), and equal amounts (5.5 %) of larvae of chironomids and oligochaetes. Then follow *Coleoptera* i., *Trichoptera* l., *Eurycercus, Simulidae* i., etc. Among the identified animals the larvae of chironomids formed the largest number, viz. 466 individuals in a volume of identified stomach contents of 11,5 cubic centimetres; they were followed by *Ephemeroptera* l., *Eurycercus, Trichoptera* i., *Oligochaeta,* etc. (see Tab. X).

According to Tab. X the food of the char is composed in the following way: *Chironomidae* l. 25.8 per cent, *Eurycercus* 19.4, *Ephemeroptera* l. 9.1, *Oligochaeta* 5.8, *Chironomidae* i. 2.2 per cent, *Trichoptera* l. and i., etc. The calculation of numbers in identified stomach contents (6,8 cubic centimetres) resulted in the following order: *Chironomidae* l. 2,424 individuals, *Eurycercus* 2,403, *Ephemeroptera* 231, *Heterocope* 82 individuals, etc.

A comparison between trout and char (Tables X) shows the food of the char to agree better with the fauna established in the former delta by the bottomsampling in 1954 (Tab. V—X). This agrees also with the fact that the char has been caught mainly in the former delta, while the trout was caught in the shallower regions outside the delta.

Remarkable is the large percentage, by number as well as by volume, of the *Ephemeroptera* l. which was not found in the examination of the bottom in 1954, but which might very well have existed in the shallower regions, where the sampling was not carried out on an equally extensive scale.

In 1949 *Siphlonurus* sp. formed the largest group of the *Ephemeroptera* in the delta. Also in the stomach samples we have mainly to do with this genus. It swims very well, and has powerful extremities by means of which it can move also upon the bottom (DAHL 1930). It is therefore conceivable that just *Siphlonurus* sp. finds less difficulty in adapting itself according to the changes of water-level occasioned by a regulation. There exists, however, a great difference (Tab. X) between the occurrence expressed in per cent of *Ephemeroptera* l. in trout (26 %) and char (9 %) respectively. This suggests that *Ephemeroptera* dwell mainly upon the new bottoms outside the former delta, since the trout have been caught in water of 1—6 metres' depth.

In July 1949 *Trichoptera* l. represented the highest percentage by volume in the stomach contents of the fish. In 1957 they form only 2.6 per cent in trout, and 1.2 per cent in char. The volume (p+i) expressed as percentage is, however, greater in 1957, and it is therefore conceivable that we have to do with different species in the two cases, as in 1949 the majority of the species of *Trichoptera* swarmed at the end of August. The *Trichoptera* l. found in the samples of 1954 (Tab. V, sample III) exhibited a decrease compared with 1949 (Fig. 20). To judge from the differences expressed in per cent of the stomach content in trout and char the distribution of *Trichoptera* l. does not seem to be so very unequal, but there exists a preponderance for occurrence in trout stomachs and consequently in shallower water.

In July 1949 *Chironomidae* l. and i. formed 1.5 and 0.4 per cent, respectively of the volume of the food, yet in 1957 the figures were 5.5 and 1.1 per cent for trout and 25.8 and 2.2 per cent for char. This illustrates at the same time the great difference between trout and char with regard to this group of consumed animals.

According to the bottom sampling in 1954 it was just the *Chironomidae* which in the delta exhibited an increase compared with August 1949 (Tab. IV and V—VIII). This is now corroborated also by the examinations of the stomach contents from 1957.

With regard to the Oligochaeta the consumption was in 1957 for trout 5.5 per cent, and for char 5.8 per cent (Tab. X). In accordance with what has appeared from the discussion above the bottom samples showed an increase of the fauna of the *Oligochaeta* after the damming-up. This is now corroborated also by the choice of food of the fish, since the consumption of *Oligo-*

chaeta by the trout in the delta of Sannarån amounted in 1949 to 0.3 per cent. LELLÁK (1957) carried out experiments in south-western Bohemia concerning the grazing of the bottom fauna by carp which was shut up in cages in a couple of ponds at different depths. In the course of these experiments he established differences in the degree of grazing with regard to *Chironomidae* and *Oligochaeta,* and found that "Die Zugänglichkeit der Bodentierwelt für die Fische ist aber von der Art des Substrats und von der Lebensweise der einzelnen Zugehörigen der Bodenfauna abhängig". In the littoral zone, where the hard substratum prevented the animals from hiding, they were consumed to 50.6 and 56.6 per cent in the two ponds, respectively. In soft substratum LELLÁK found the percentage to be 41.8 and 47.2 per cent for the respective ponds. The larvae of the chironomids were consumed more intensely than those of the oligochaetes which live deeper in the mud. This is also confirmed by the examinations of the contents of char stomach from 1957.

Since *Gammarus lacustris* could not be found again in the stomach samples from both trout and char, we are forced to suppose according to the foregoing that this group of animals has been exterminated.

For trout the consumption of *Eurycercus* appears to be greater in 1957 (2.6 %) than in July 1949 (0.1 %). This corroborates an increase for *Eurycercus* in the neighbourhood, if also the contribution of the char (19.4 %) is included. This would agree with the examinations in 1954 of the fauna of the bottom, when according to the foregoing the samples from naked bottoms, showed an increase of the stock of *Eurycercus.* Probably the fish find less difficulty in getting hold of *Eurycercus* l. after regulation which now has no denser vegetation to cling to.

If we compare the years 1949 and 1957 we find the terrestrial food (Tab. X) to form in the later year only a very small portion. This circumstance can doubtlessly be explained to a certain extent by the fact that as a result of the damming-up the distance between the delta and the forest region has increased.

The material of the investigation is of too special a nature to permit the determination of the effect of the regulation upon the bottom fauna of a lake, since the comparison stands between a delta before the regulation and the former delta which after the regulation is situated on the bottom of the lake far from the beach. Certain similarities with the results obtained by HUITFELDT-KAAS (1935) in connection with the examinations of Norwegian regulations of lakes could nevertheless be observed. In 1928 this author carried out investigations into the food of the fish in Tunhövdfjord which had earlier been examined by DAHL in 1920 and 1923. On this occasion he found that *Trichoptera, Ephemeroptera,* and *Sialidae,* the disappearance of which after the regulation had been asserted by DAHL, were found in great numbers in the stomachs of the fishes five years after the regulation.

HUITFELDT-KAAS believed this to be due to imperfect investigations by DAHL after the regulation, imperfectious which DAHL himself had pointed out. For the disappearance of the gammarids both DAHL and HUITFELDT-KAAS arrived at the same results. Also in the delta of Sannarån the same result was obtained, since gammarids could not be found in the samples of 1954 and 1957. *Trichoptera* were found again in the samples from the delta of 1954 and 1957 showing, in agreement with HUITFELDT-KAAS, that this group had not been exterminated. It lies close at hand to find a kind of explanation of the better representation of certain groups of animals in the samples of a later investigation after the damming-up, e.g. in the assumption that after five years a certain equilibrium had been attained. This can depend upon that, e.g., the erosion of surrounding loose soils has ceased, that the sedimentation has to a certain extent become stabilized, that the decomposition of plant material from the old and the newly drowned bottoms, resulting in a decreased consumption of oxygen at the bottom, has come to an end.

One additional point of view can be applied to the conditions in the delta in 1957, viz. five years after the damming-up. Investigations in connection with the damming of valleys (WUNDSCH 1949) and the analysis of the growth of the fish in regulated lakes (RUNNSTRÖM 1951) have shown that in general production increases during the first years after the regulation of a lake, but that this is followed by a reverse. Other investigations at the Institute for Freshwater Research (NILSSON 1955) into the choice of food of char and trout, present together in a lake, have shown that during years with poor production of food niches are easily formed on account of the competition for food so that the char stays in deeper water, and consumes more planktonic food than the trout which stays in shallower water. If food, suitable for both trout and char, is available in abundance no niches are formed for the two types of fish (NILSSON 1955). This situation ought to be typical for the first years of the damming-up, and in 1957 belonged to the past.

Table X show a reduction in the number of consumed groups of animals in the diet of the char in 1957, if we compare it with that of the trout. The former has furthermore consumed considerably more planktonic and semiplanktonic food than the latter. The char fed mainly on *Chironomidae* l. and *Eurycercus,* while the main food of the trout consisted of *Ephemeroptera* l. and *Trichoptera* i. According to NILSSON (1955) this should point to the existence of a certain competition between trout and char, and this in turn should indicate that the food supply is not especially abundant. In the foregoing also a certain impoverishment in bottom animals of the littoral after the regulation has been established.

3. Changes in the growth rate of trout in relation to the regulation

The production of fish food in a lake can be measured also indirectly by measuring the growth zones of the scales of the fish, the growth of the

Table XII. The mean air temperature (centigrade) in Gäddede 1948—1956.

Months	1948	1949	1950	1951	1952	1953	1954	1955	1956
June	13.7	13.2	12.7	10.1	10.6	18.0	12.9	10.8	12.2
July	18.6	15.2	15.5	12.7	14.5	15.3	16.9	16.5	15.8
August	13.0	13.7	17.9	16.5	12.4	15.5	14.6	16.5	12.5

scales standing in a certain relation to the growth of the fish. It is universally known that the growth of fish is very susceptible to external influences. It varies with the supply of food with the result that years with scarcity of food result in poor growth, and *vice versa.* This relation is, however, modified by quite a number of factors, e.g. competition both within the species and between species (size of year classes), differences with regard to the stationariness, migrations, recruitment, etc., in order to mention only some of the factors which can produce a direct effect.

Before continuing the discussion we shall examine Fig. 31 in which the growth of some trout belonging to different year classes from the delta of Sannarån or its neighbourhood before and after the damming-up is marked off along the y-axis. Fig. 31 shows the growth to be relatively equivalent for the years 1948—1952. A very important factor, however, is the temperature which must be taken into consideration in the discussion of growth diagrams in connection with the effect of the damming-up. Warm springs and summers are known to produce broad annual rings upon the scales (SVÄRDSON 1951, RUNNSTRÖM 1957, and others). In 1952 the spring was cold. In the area of Gäddede, the area with official meteorological records which most closely agrees in the climate with the delta of Sannarån, the mean temperature for June was +10.6°C (Table XII), and the damming-up, which was not complete in this year (Fig. 27), was not started until the autumn. As at this time the curve for the production of the bottom animals is dropping, the effect of the damming-up could not be expected to have any greater influence upon the growth. In 1953, however, June was very warm. For the area of Gäddede the mean temperature was then 18.0°C (Table XII), and the damming-up was complete. For these reasons we can count here with an accumulated result of the warm early summer and of the effect of the damming-up, leading to the marked increase of growth during 1953 (Fig. 31). In 1954 the growth is still good, but in the area of Gäddede the mean temperature for June of this year is 12.9°C (Table XII). For this reason the accumulated result of rise of temperature and effect of the damming-up is not as large as in the preceding year. This is obvious also from Fig. 31 which shows a somewhat feebler growth. The growth is nevertheless above normal which ought in this case to be attributable to the damming-up. After 1955 a further decrease in growth can be noticed, probably indicating

Table XIII. From Geng 1925.

Name	Wärmewert für ein Tier cal.	Name	Wärmewert pro 1 g. Subst. cal.
Macrocorixa	131,4	Regenwurm	4841,0
Lestes	115,4	Weißfische	4724,0
Dreissensia	87,6	Physa font.	4699,5
Phyca font	73,8	Chironomus plum.	4687,0
Bythinia tentac.	62,3	Carinogammarus	4443,5
Ephemera vulg.	46,5	Naucoris cim.	4248,0
Leptocerus sp.	42,6	Daphnia pulex	3981,0
Carinogammarus	29,3	Gammarus pulex	3921,0
Limnaea ovata	26,7	Limnophilus rh.	3808,0
Agrion	24,8	Asellus aqu.	3763,0
Sphaerium sp.	21,9	Daphnia magna	3547,0
Gammarus pulex	20,4	Limnaea stagn.	1635,5
Asellus aqu.	19,8	Limnaea auric.	1593,0
Cloëon dipt.	12,7	Bythinia tent.	1357,0
Chironomus plum.	12,0	Paludina vivip.	1309,0
Ameisenpuppen	11,0	Limnaea ovata	1307,0
Chironomus greg.	3,4	Planorbis carinatus	1300,5
Daphnia magna	1,3	Sphaerium sp.	1296,5
Daphnia pulex	0,13	Leptocerus sp.	838,5
Weißfische	4801,5	Dreissensia polym.	640,5
Phryganea grandis	1024,0	Cloëon dipterum	6039,0
Paludina vivipara	1017,0	Phryganea grandis	5922,0
Limnaea stagn.	1011,0	Lestes	5683,0
Limnaea auric.	267,8	Ephemera vulg.	5438,0
Perla cephalotes	261,4	Macrocorixa	5213,0
Regenwurm	217,8	Agrion	5208,5
Limnophilus rh.	175,2	Perla cephalotes	5165,5
Ameisenpuppen	4991,0	Chironomus gr.	5101,0

that the effect of the damming-up is weakening, and that a certain stabilization has started to establish itself.

The growth of the fish usually increases in the first years after a regulation, as we have seen also here. This is due to the ample addition of food derived from the overflooded areas. Runnström (1951) has demonstrated that in Lake Torrön the char had gained in growth during the first few years after the regulation, but that this period was followed by one of diminished growth. Frost (1956) who has studied the damming-up of lakes in England found in Haweswater an increased growth of thout during the first years after the damming-up.

A special aspect of the problem of regulation shall be discussed here. When in 1954 samples of the bottom fauna were taken, a decrease in the number of species was found in accordance with the foregoing discussion. It was, however, also observed that in certain species the number of individuals had increased. We are now faced with the problem, whether or not the calorific value of a certain type of food, which has disappeared, can be replaced, e.g. by a larger number of other animals with inferior caloric value, and whether or not the growth rate can be maintained in this way. Appetite and ability of digesting the food, both dependent on the temperature, are of course of importance in this connection. In order to obtain a certain insight into such problems we have to turn to literature. MILLER (1936) has examined several species of fish, e.g. trout (*Salmo trutta fario*) in order to find out, whether or not the fat of the consumed animals could be transformed without major losses into the specific fat of the fish. This was found to be the case. For trout +9°C was found to be the most advantageous temperature for the digestion of the food (CORNELIUS 1933). Table XIII in which the figures for the calorific value of some common animals consumed by fish are determined has been taken from GENG (1925). If in accordance with GENG *Gammarus pulex* is chosen as the type for the caloric value of the larger crustaceans, Tab. XIII gives on comparison with the earth-worm (*Oligochaeta*) as type of the larger *Oligochaeta* the calorific values of 3,921.0 and 4,841.0, respectively, for 1 gram of substance. This shows that the lack of *Gammarus* can be replaced by a lesser weight of *Oligochaeta,* since this group of animals possesses a higher calorific value. As far as calories are concerned the great upswing of the *Oligochaeta* can thus more than well replace the disappearance of the gammarids. The representatives of the *Ephemeroptera* have a high caloric value, and if in accordance with GENG (1925) *Cloëon dipterum* is chosen as type of the small *Ephemeroptera,* then Tab. XIII gives 6,039.0 calories for 1 gram of substance, and 12.7 for one animal. The corresponding values for the group of *Chironomus plumosus* are according to Tab. XIII 4,687.0 and 12.0 calories, respectively. The group of *Chironomus plumosus,* which in 1954 has increased in the delta, ought to be able to replace the *Ephemeroptera.* Taking into consideration that the animals which have increased after he damming-up e.g. *Oligochaeta* and *Chironomidae,* have relatively high calorific values, they ought of their great numbers after the damming-up to be more than able to make good the disappearance of e.g. *Ephemeroptera, Gammarus,* etc. There exists, however, no doubt that the fish have to spend more energy in the catching of a larger number of smaller animals, e.g. oligochaetes, than in that of a smaller number of larger prey, e.g. *Gammarus,* provided that both occur with the same density.

V. Summary

One of the most extensive regulations of lakes of later times in Sweden has been carried out in Lake Borgasjön, belonging to the drainage system of Ångermanälven. The amplitude of the regulation was 18 metres.

1. An examination of the fauna in the uppermost one of the deltas in the River Sannarån, connecting Borgasjön with the more elevated Lake Sannaren, was carried out in 1948 and 1949, prior to the regulation of the lake and,

later, in 1954 and 1957, when the lake had been under the influence of the regulation for two and five years, respectively. The interest was centered on the epifauna in the months June, July, and August 1949 before the regulation, but also bottom fauna and fish fauna were studied.

2. Samples of the epifauna were taken from three vegetational regions containing *Carex vesicaria, Myriophyllum alterniflorum,* and *Ranunculus peltatus.*

3. For the distribution of the animals in the vegetational belts the factor of nutrition seemed to play an outstanding rôle. The epifauna was richest in the areas with *Myriophyllum alterniflorum,* where also the representation of the epiphytes was most aboundant. Upon *Carex vesicaria* the epiphytes were fewest, and also the epifauna was scantiest there. *R. peltatus* occupied a place intermediate between the two above-mentioned.

4. The distribution of the animals in the different plant biotopes also varied with the seasons.

5. Bottoms free from macrophytes proved to contain a much smaller number of species than those covered with vegetation.

6. In 1954, the third year of regulation, the former vegetational belts in the delta had been completely destroyed.

7. A great part of the fauna (*Amphipoda Acarina, Plecoptera, Ephemeroptera Neuroptera, Coleoptera,* and the majority of the *Trichoptera*) had completely disappeared from the delta.

8. A shifting in the dominance as existing in 1949, before regulation, for *Phyllopoda, Ephemeroptera, Oliochaeta, Diptera,* and *Trichoptera* towards *Oligochaeta, Diptera* and *Nematoda* was observed after regulation.

9. In 1949 the delta of Sannarån was an appreciated dwelling place of growing trout most of which belonged to the age group of 3—4 years. It is suggested that in the vegetational belts the delta offered good hiding places and a good accumulation of prey.

10. The samples of stomachs, examined in 1949, supplied a fairly good picture of the conditions existing in the delta. The seasonal variation which in the foregoing had been established for the animals serving as food were reproduced also in the samples of stomachs.

11. During the first time after the regulation the fish seemed to shun the former delta, and no fish were obtained in 1954.

12. In 1957, five years after regulation, the former delta was invaded by char. Trout, however, stayed in shallower areas outside the delta.

13. The examination in 1957 of stomach samples from trout and char showed that the char consumed more planktonic food than the trout, the former feeding mainly on Chironomidae l. and Eurycercus. The main food of the trout consisted of *Ephemeroptera* l. and *Trichoptera* i. The competition for food between trout and char is suggested to indicate that the food

supply is not especially abundant. Bottom samples 1954 also showed a certain impoverishment in bottom animals after regulation.

14. Also the growth of the trout was examined by measuring the growth zones of the scales of the fish belonging to different year classes from the delta of Sannarån or its neighbourhood before and after regulation. The increased growth of the fish observed during the first years after the damming-up was suggested to be due mainly to the ample addition of food derived from flooded areas. After 1955 a decrease in the growth could be noticed, probably indication that the effect of damming-up was weakening, and that a certain stabilisation had began to establish itself.

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